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Integrative systematics of northern and Arctic nudibranchs of the genus *Dendronotus* (Mollusca, Gastropoda), with descriptions of three new species

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The taxonomy of common northern nudibranch molluscs of the genus *Dendronotus* in the vast cold regions of Eurasia remains largely unknown. Abundant material collected in many localities from the Barents Sea, via the Arctic region, to the north-west Pacific was analysed for the first time. An integrated approach combining morphological and ontogenetic data with molecular four-gene (*COI*, *16S*, *H3*, and *28S*) analysis reveals seven species, including three previously undescribed. *Dendronotus frondosus* (Ascanius, 1774) and *Dendronotus dalli* Bergh, 1879 were commonly considered as amphiboreal species; however, according to this study they are restricted to the North Atlantic and the North Pacific, respectively. In the north-west Pacific two new species were discovered, ***Dendronotus kamchaticus* sp. nov.** and ***Dendronotus kalikal* sp. nov.**, that are externally similar to *D. frondosus*, but that show significant distance according to molecular analysis and are considerably different in radular morphology. In the North Atlantic a new species ***Dendronotus niveus* sp. nov.**, sibling to North Pacific *D. dalli*, is revealed. The separate status of North Atlantic *Dendronotus lacteus* (Thompson, 1840) is confirmed, including considerable range extension. The essential similarity of early ontogenetic stages of radular development common for species with disparate adult radular morphology (such as *D. frondosus* and *D. dalli*) is shown, and its importance for taxonomy is discussed.

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ADDITIONAL KEYWORDS: molecular analysis – molluscs – morphology – ontogeny – phylogenetics – taxonomy.

INTRODUCTION

The opisthobranch molluscs of the genus *Dendronotus* are among the most common shallow-water bottom marine invertebrates of the northern hemisphere. Opisthobranchs have emerged as a model group in taxonomic, phylogenetic, developmental, physiological, and molecular studies (Wägele *et al*., 2013). During the last two decades traditional taxonomic practice has been challenged (Godfray, 2002), and molecular methods have revealed new perspectives for phylogenetic analysis (e.g.

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Yang & Rannala, 2012; Johnson & Gosliner, 2012; Carmona *et al*., 2013) and have uncovered numerous cryptic species in different metazoan groups (e.g. Barco *et al*., 2013; Jörger & Schrödl, 2013). Recently, our understanding of the necessity of integrative approaches has been growing (e.g. Dayrat, 2005; Valdecasas, Williams & Wheeler, 2008; Schlick-Steiner *et al*., 2010; Huelsken *et al*., 2012; Ahmadzadeh *et al*., 2013; Krug *et al*., 2013; Ohnheiser & Malaquias, 2013; Carmona *et al*., 2014). Here, using numerous specimens sampled in the North Atlantic, Arctic, and North Pacific regions, we show how morphological data coupled with molecular and ontogenetic information may contribute to our understanding of the taxonomy and phylogeny of a group.

Taxonomic history of the genus *Dendronotus*

The genus *Dendronotus* was established in the mid-19th century (Alder & Hancock, 1845) with the type genus *Dendronotus frondosus* (Ascanius, 1774). This species was described by Peter Ascanius among the polychaete genus *Amphitrite*. Prior to the separation of the genus *Dendronotus*, a number of North Atlantic species have been described under various names (e.g. *Doris arborescens* Müller, 1776, *Tritonia reynoldsii* Couthouy, 1838, and *Tritonia felina* Alder & Hancock, 1842). The initial placement of the polychaete has some influence after the formal creation of the genus *Dendronotus* (e.g. in the name *Amphitridea fabricii* Kröyer, 1847).

Early in his career Rudolph Bergh (1863, 1886) described the genus *Campaspe*, which was later synonymized with *Dendronotus* by Vayssiere (1913). Several additional species from the North Atlantic were described [e.g. *Dendronotus luteolus* LaFont, 1871 and *Dendronotus lacteus* (Thompson, 1840)]. James Cooper (1863) described the first Pacific species, *Dendronotus iris* Cooper, 1863. Its validity was further confirmed (Odhner, 1936) and unusual behaviour patterns revealed (Wobber, 1970; Shaw, 1991; Behrens, 2005). Bergh (1879, 1884, 1886, 1891) provided anatomical information on the common species *D. frondosus* and described another Pacific species *Dendronotus dalli* Bergh, 1879. Despite the initial diversity in the names, almost all mentioned species were later considered as synonyms of the single common species *D. frondosus*, (including *D. lacteus* and the 'genus' *Campaspe*; see Odhner, 1936, 1939). The only exceptions were the North Atlantic species *Dendronotus robustus* Verrill, 1870 and the North Pacific species *D. iris*. Thus, until recently *D. frondosus* was commonly regarded as an amphiboreal species, with a very broad range extending from the European seas and the Arctic Ocean to California and Chile (Robilliard, 1970, 1975; Behrens, 1980, 1991; McDonald, 1983, 2009; Roginskaya, 1987; Schrödl, 2003).

In the mid-20th century Frank Mace MacFarland in his opus magnum (MacFarland, 1966) added several more North Pacific species of the genus *Dendronotus*, including *Dendronotus albus* MacFarland, 1966, *Dendronotus subramosus* MacFarland, 1966, and *Dendronotus venustus* MacFarland, 1966. The diversity and distinctness of the North American *Dendronotus* species was confirmed in a detailed morphological review of this genus (Robilliard, 1970); however, *D. venustus* was commonly regarded as a synonym of the Atlantic *D. frondosus*, even in the North American literature (McDonald, 2009). The only single record of nudibranch molluscs from the deep-sea hydrothermal vents includes a new species of the genus *Dendronotus* (Valdes & Bouchet, 1998). Recently two new species, *Dendronotus regius* Pola & Stout, 2008 and *Dendronotus noachi* Pola & Stout, 2008 from the tropical East Pacific have been described (Pola & Stout, 2008). An enigmatic taxon from the East Pacific, *Pseudobornella orientalis* Baba, 1932 was considered a species of the genus *Dendronotus* (Pola & Gosliner, 2010). Considerable changes also occurred in the taxonomy of North Pacific species. A molecular study showed minor but reliable differences between Pacific and Atlantic populations of *D. frondosus* (Stout, Pola & Valdés, 2010). The MacFarland's name *D. venustus* was therefore restored. The validity of North Atlantic species *D. lacteus* was confirmed based on allosyme electrophoresis and morphological data (Thollesson, 1998). Some other North American species (e.g. *Dendronotus nanus* Marcus & Marcus, 1967 and *Dendronotus diversicolor* Robilliard, 1970) were instead shown to be synonyms of *D. iris* and *D. albus*, respectively (Stout *et al*., 2010). Another North Pacific species, *Dendronotus patricki* Stout, Wilson & Valdés, 2011, has been described from the deep sea off California (Stout, Wilson & Valdés, 2011). It therefore may imply that the North Pacific fauna conceals more cryptic diversity of the genus; however, the vast cold water regions of the north-western Pacific have not yet been studied sufficiently.

MATERIAL AND METHODS

Sample data

Material for this study was obtained from various expeditions and fieldwork, and included 341 specimens belonging to the genus *Dendronotus*. All specimens were deposited in the Zoological Museum of Lomonosov Moscow State University (ZMMU), except for two paratypes of *Dendronotus niveus* sp. nov., which were obtained from a subsidiary of ZMMU at the White Sea Biological Station (WS). The full information of material used is presented in Table 1. Fresh specimens of *Dendronotus kamchaticus* sp. nov., *D. dalli*, and *Dendronotus kalikal* sp. nov. were collected along the

Table 1. Collection data with GenBank assession numbers for specimens used for molecular analysis

Species	Locality	Voucher no.	GenBank assession numbers				No.	Depth (m)	Date	Collector
			COI	*16S*	*H3*	*28S*				
Dendronotus dalli	North-west Pacific, Kamchatka, Starichkov Island	ZMMU Op-294	KC660023	KC611294	KC660039	KC660007	2 spcs	7–12	14.viii.2008	T.A. Korshunova, A.V. Martynov
D. dalli	North-west Pacific, Kamchatka, Starichkov Island	ZMMU Op-295	KM397001	KM397083	KM397094	KM397042	1 spc.	7–12	19.viii.2008	T.A. Korshunova, A.V. Martynov
D. dalli	North-west Pacific, Kamchatka, Starichkov Island	ZMMU Op-329					2 spcs	10–15	5.x.2006	N.P. Sanamyan
D. dalli	North-west Pacific, Kamchatka, Starichkov Island	ZMMU Op-330	KM396999	KM397081	KM397102	KM397040	1 spc.	22	15.ix.2012	N.P. Sanamyan
D. dalli	North-west Pacific, Kamchatka, Starichkov Island	ZMMU Op-331	KM397000	KM397082	KM397103	KM397041	1 spc.	22	15.ix.2012	N.P. Sanamyan
D. dalli	Bering Sea, RV 'Healy', sta. 96. 62°973.766′N, 176°061.99′E	ZMMU Op-351					1 spc.	67	30.v.2006	B.I. Sirenko
D. dalli	Bering Sea, RV 'Healy', sta. 1. 61°346.216′N, 171°947.32′W	ZMMU Op-352					2 spc.	60	9.v.2006	B.I. Sirenko
D. dalli	Bering Sea, RV 'Healy', sta. 50. 64°349.669′N, 168°625.98′W	ZMMU Op-353					1 spc.	33	22.v.2006	B.I. Sirenko
D. dalli	Bering Sea, RV 'Healy', sta. 64. 65°214.059′N, 168°385.94′W	ZMMU Op-354					1 spc.	48	25.v.2006	B.I. Sirenko
Dendronotus frondosus	Norway, of the Sognefjord, Gulen Dive Resort	ZMMU Op-380	KM396976	KM397056	KM397111	KM397017	neotype		18.iii.2014	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-297					12 spcs	0.2–0.3	16.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-298	KM396985	KM397067	KM397095	KM397025	4 spcs	10	9.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-299	KM396984	KM397066	KM397096	KM397026	9 spcs	0.4	3.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-300					2 spcs	0.4	20.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-301					11 spcs	0.5	2.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-302					7 spcs	0.2–0.4	5.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-303					7 spcs	0.4–0.8	17.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-304					9 spcs	0.5	6.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-305					1 spc.	0.2	18.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-306					1 spc.	8	24.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-307					16 spcs	0.2–0.4	4.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-308					3 spcs	5	11.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-309					2 spcs	4	15.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-310					1 spc.	5	13.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-311					1 spc.	5	29.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-312					1 spc.	0.2	10.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-313					2 spcs	0.2–0.3	16.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-314					1 spc.	4	8.viii.2012	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Varangerfjord	ZMMU Op-315					8 spcs	0.2–0.4	6.ix.2012	T.I. Antokhina
D. frondosus	Barents Sea, Varangerfjord	ZMMU Op-316					8 spcs	0.2–0.5	2.ix.2012	T.I. Antokhina
D. frondosus	White Sea, Kandalaksha Bay, Velikaya Salma Strait	ZMMU Op-317	KM396978	KM397060	KM397097	KM397019	3 spcs	1–2	13.ix.2011	I.A. Ekimova
D. frondosus	White Sea, Kandalaksha Bay, Velikaya Salma Strait	ZMMU Op-318					5 spcs	0.3	12.ix.2011	I.A. Ekimova
D. frondosus	White Sea, Kandalaksha Bay, Velikaya Salma Strait	ZMMU Op-290	KC660028	KC611280	KC660040	KC660008	10 spcs	0.1–0.2	2.vii.2012	I.A. Ekimova
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-291	KC660030	KC611281	KC660041	KC660009	4 spcs	0.1–0.2	vii.2008	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Plohie Chevry Bay	ZMMU Op-292	KC660031	KC611282	KC660042	KC6600010	5 spcs	0.5–0.7	vii.2008	T.A. Korshunova, A.V. Martynov
D. frondosus	White Sea, Kandalaksha Bay, Velikaya Salma Strait	ZMMU Op-293	KC660029	KC611283	KC660043	KC6600011	4 spcs	0.1–0.2	13.ix.2011	I.A. Ekimova

Table 1. *Continued*

Species	Locality	Voucher no.	GenBank assession numbers				No.	Depth (m)	Date	Collector
			COI	*16S*	*H3*	*28S*				
D. frondosus	White Sea, Kandalaksha Bay, Velikaya Salma Strait	ZMMU Op-319					10 spcs	10–12	25.iv.2007	N.A. Chervyakova
D. frondosus	White Sea, Kandalaksha Bay, Velikaya Salma Strait	ZMMU Op-320					7 spcs	7–10	14.ix.2011	A.A. Semenov
D. frondosus	White Sea, Kandalaksha Bay, Velikaya Salma Strait	ZMMU Op-321					6 spcs	10	17.ix.2011	A.A. Semenov
D. frondosus	White Sea, Kandalaksha Bay, Kartesh	ZMMU Op-322					5 spcs	0.2–0.6	5.vi.2008	T.A. Korshunova, A.V. Martynov
D. frondosus	White Sea, Kandalaksha Bay, Velikaya Salma Strait	ZMMU Op-323					5 spcs	7–10	3.vi.2009	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-324	KM396980	KM397062	KM397098	KM397021	7 spcs	0.3–0.4	5.viii.2005	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-325	KM396981	KM397063	KM397099	KM397022	8 spcs	0.5–0.7	4.viii.2005	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Plohie Chevry Bay	ZMMU Op-326	KM396982	KM397064	KM397100	KM397023	8 spcs	0.3–0.4	6.viii.2005	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Plohie Chevry Bay	ZMMU Op-327	KM396983	KM397065	KM397101	KM397024	6 spcs	1	15.viii.2005	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-328					3 spcs	2–5	12.viii.2006	T.A. Korshunova, A.V. Martynov
D. frondosus	Barents Sea, R/V 'Dalnie Zelentsy', sta. UR-22, 69°02′N, 57°07.1′E	ZMMU Op-359	KM396979	KM397061	KM397110	KM397020	1 spc.	12	7.x.2012	O.L. Zimina
D. frondosus	Barents Sea, R/V 'Dalnie Zelentsy', sta. MB-15, 69°14.3′N, 57°39.5′E	ZMMU Op-381					2 spcs	19	18.vii.2013	O.L. Zimina
D. frondosus	Barents Sea, R/V 'Dalnie Zelentsy', sta. MB-2, 68°56.9′N, 57°56.9′E	ZMMU Op-382	KM396977	KM397050	KM397112	KM397018	5 spcs	13	22.vii.2013	O.L. Zimina
***Dendronotus kalikal* sp. nov.**	North-west Pacific, Kamchatka, Starichkov Island	ZMMU Op-283	KC660024	KC611284	KC660044	KC660012	holotype	14–16	23.viii.2009	N.P. Sanamyan
***D. kalikal* sp. nov.**	North-west Pacific, Kamchatka, Starichkov Island	ZMMU Op-284	KC660025 KC660026 KM396988	KC611286 KC611285 KM397070	KC660046 KC660045 KM397092	KC660013 KC660014 KM397029	5 paratypes	14–16	15.ix.2009	N.P. Sanamyan
***D. kalikal* sp. nov.**	Bering Strait, R/V 'Healy', sta. 1. 61°346.216′N, 171°947.32′E	ZMMU Op-285	KC660027	KC611287	KC660047	KC660015	1 paratype	60	9.v.2006	B.I. Sirenko
***D. kalikal* sp. nov.**	North-west Pacific, Kamchatka, Avachinsky Bay	ZMMU Op-349	KM396986 KM396987	KM397068 KM397069	KM397108 KM397109	KM397027 KM397028	11 paratypes	20–22	15.ix.2012	N.P. Sanamyan
***Dendronotus kamchaticus* sp. nov.**	North-west Pacific, Kamchatka, Cape Baraniy	ZMMU Op-245	KC660032	KC611288	KC660048	KC660016	holotype	7	15.vi.2010	A.A. Semenov
***D. kamchaticus* sp. nov.**	North-west Pacific, Kamchatka, Avachinsky Bay	ZMMU Op-246	KC660033 KM396989 KM396990	KC611289 KM397071 KM397072	KC660049 - -	KC660017 KM397030 KM397031	4 paratypes	7	6.viii.2008	T.A. Korshunova, A.V. Martynov
***D. kamchaticus* sp. nov.**	North-west Pacific, Kamchatka, Avachinsky Bay	ZMMU Op-247	KM396991 KM396992	KM397073 KM397074	- -	KM397032 KM397033	3 paratypes	7	viii.2008	T.A. Korshunova, A.V. Martynov
Dendronotus lacteus	Norway, off the Sognefjord, Gulen Dive Resort	ZMMU Op-383	KM396971 KM396972	KM397054 KM397055	KM397113 KM397114	KM397012 KM397013	2 spc.	25	19.iii.2014	B. Picton, T.A. Korshunova, A.V. Martynov
D. lacteus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-286	KC660034	KC611290	KC660050	KC660018	2 spcs	10–12	1.viii.2007	O.V. Savinkin
D. lacteus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-287	KC660035	KC611291	KC660051	KC660019	1 spc.	7–10	7.viii.2005	O.V. Savinkin
D. lacteus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-288	KM396975	KM397059	KM397093	KM397016	1 spc.	10	6.viii.2012	T.A. Korshunova
D. lacteus	Barents Sea, Spitsbergen	ZMMU Op-289					2 spcs	10–20	viii.2009	–
D. lacteus	Barents Sea, R/V 'Johan Hjort', sta. 23,78°09.1000′N, 14°49.4485′E	ZMMU Op-332					1 spc.	166	18.viii.2012	O.S. Lyubina
D. lacteus	Barents Sea, R/V 'Johan Hjort', sta. 347, 75°06.5276′N, 21°10.3661′E	ZMMU Op-333	KM396974	KM397058	KM397104	KM397015	2 spcs	45	27.viii.2012	O.S. Lyubina
D. lacteus	Barents Sea, R/V 'Johan Hjort', sta. 451, 76°54.722′N, 22° 33.279′E	ZMMU Op-334					1 spc.	97	08.ix.2012	O.S. Lyubina

D. lacteus	Barents Sea, R/V 'Johan Hjort', sta. 395, 76°23.255′N, 25°33.438′E	ZMMU Op-335	KM396973	KM397057	KM397105	KM397014	1 spc.	103	27.ix.2012	O.S. Lyubina
D. lacteus	Barents Sea, R/V 'Johan Hjort', sta. 342, 74°52.974′N, 16°46.176′E	ZMMU Op-336					2 spc.			O.S. Lyubina
D. lacteus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-337					1 spc.	7–10	7.viii.2005	O.V. Savinkin
D. lacteus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-338					2 spc.	5	15.viii.2012	T.A. Korshunova, A.V. Martynov
D. lacteus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-339					1 spc.	10	9.viii.2005	T.A. Korshunova, A.V. Martynov
D. lacteus	Barents Sea, R/V 'Romuald Muklevich', sta. 115, 71°30.010′N, 44°58.580′E	ZMMU Op-340					1 spc.	70	29.viii.2003	P.A. Lyubin
D. lacteus	Barents Sea, R/V 'Romuald Muklevich', sta. 110, 69°00.670′N, 44°58.899′E	ZMMU Op-394					1 spc.	58–60	28.viii.2003	P.A. Lyubin
D. lacteus	Franz Josef Land, Wilton Island, 80°34.6′N, 54°19.9′E	ZMMU Op-384					1 spc.	18–28	23.viii.2013	S.D. Grebelny
D. lacteus	Franz Josef Land, Bliss Island, 80°22.3′N, 54°39.6′E	ZMMU Op-385					1 spc.	10–20	24.viii.2013	O.V. Savinkin
D. lacteus	Franz Josef Land, Pioneer Island, 80° 38,198 N, 58°54,033 E	ZMMU Op-386					2 spcs	15–23	17.viii.2013	O.V. Savinkin
D. lacteus	Franz Josef Land, Northbrook Island, 79°56.6′N, 50°05.5′E	ZMMU Op-387					3 spcs	18–20	26.viii.2013	S.D. Grebelny
D. lacteus	Franz Josef Land, Heiss Island, 80°34′N, 57°41′E	ZMMU Op-388					3 spcs	9–25	13.viii.2013	O.V. Savinkin
D. lacteus	Franz Josef Land, Howen Island, 81°31′N, 58°31′E	ZMMU Op-389					1 spc.	18–31	20.viii.2013	O.V. Savinkin
***Dendronotus niveus* sp. nov.**	White Sea, Kandalaksha Bay, Velikaya Salma Strait	ZMMU Op-269	KM396996	KM397078	KM397087	KM397037	holotype	17	12.ix.2012	G.D. Kolbasova, A.V. Makarov
***D. niveus* sp. nov.**	White Sea, Kandalaksha Bay, Sidorov Island	ZMMU Op-270	KM396997	KM397079	KM397088	KM397038	5 paratypes	25	28.vii.2012	G.D. Kolbasova, N.Y. Neretin
***D. niveus* sp. nov.**	Barents Sea, Bear Island	ZMMU Op-274	KC660037 KM396993 KM396994	KC611293 KM397076 KM397075	KC660053 KM397089 KM397090	KC660021 KM397034 KM397035	3 paratypes	50–80	15.v.2007	R. Johansen
***D. niveus* sp. nov.**	White Sea, Kandalaksha Bay, Velikaya Salma Strait	ZMMU Op-271					1 paratypes	15	17.vii.2012	G.D. Kolbasova
***D. niveus* sp. nov.**	White Sea, Kandalaksha Bay, Velikaya Salma Strait	ZMMU Op-272					1 paratype	12	11.vii.2012	S.A. Gorin
***D. niveus* sp. nov.**	White Sea, Kandalaksha Bay, Velikaya Salma Strait	ZMMU Op-273					3 paratypes	17	20.vii.2012	G.D. Kolbasova
***D. niveus* sp. nov.**	Barents Sea, Canin Nos Cape, R/V 'Romuald Muklevich', sta. 110, 69°00.670′N, 44°58.899′E	ZMMU Op-275					1 paratype	58–60	28.viii.2003	P.A. Lyubin
***D. niveus* sp. nov.**	Barents Sea, R/V 'Romuald Muklevich', sta. 74, 71°00.293′N, 41°31.858′E	ZMMU Op-276					1 paratype	85	24.viii.2003	P.A. Lyubin
***D. niveus* sp. nov.**	Barents Sea, R/V 'Romuald Muklevich', sta. 49, 69°59.929′N, 37°59.614′E	ZMMU Op-277					1 paratype	153–156	19.viii.2003	P.A. Lyubin
***D. niveus* sp. nov.**	Barents Sea, R/V 'Romuald Muklevich', sta. 115, 71°30,010′N, 44°58.580′E	ZMMU Op-278					1 paratype	70	29.viii.2003	P.A. Lyubin
***D. niveus* sp. nov.**	Barents Sea, R/V 'Johan Hjort', sta. 347, 75°06.5276′N, 21°10.3661′E	ZMMU Op-279	KM396995	KM397077	KM397091	KM397036	3 paratypes	44.7	27.viii.2012	O.S. Lyubina

Table 1. *Continued*

Species	Locality	Voucher no.	GenBank assession numbers				No.	Depth (m)	Date	Collector
			COI	*16S*	*H3*	*28S*				
***D. niveus* sp. nov.**	Barents Sea, R/V 'Johan Hjort', sta. 472, 77°26.1448′N, 13°42.0457′E	ZMMU Op-280					1 paratype	41.5	13.ix.2012	O.S. Lyubina
***D. niveus* sp. nov.**	Barents Sea, R/V 'Johan Hjort', sta. 333, 75°41.3850′N, 20°49.2952′E	ZMMU Op-281					1 paratype	42	25.viii.2012	O.S. Lyubina
***D. niveus* sp. nov.**	Barents Sea, R/V 'Johan Hjort', sta. 335, 75°34.0694′N, 18°29.6825′E	ZMMU Op-282					1 paratype	119	25.viii.2012	O.S. Lyubina
***D. niveus* sp. nov.**	White Sea, Kandalaksha Bay, Velikaya Salma Strait	WS1102	KC660036	KC611292	KC660052	KC660020	1 paratype	28	30.vii.2011	A.N. Isaychev
***D. niveus* sp. nov.**	White Sea, Kandalaksha Bay, Velikaya Salma Strait	WS2005	KM396998	KM397080	KM397086	KM397039	1 paratype	18	22.vii.2012	T.I. Antokhina
***D. niveus* sp. nov.**	White Sea, Kandalaksha Bay, Velikaya Salma Strait	ZMMU Op-397					1 paratype	23	9.vi.2014	F.V. Bolshakov
Dendronotus robustus	Barents Sea, R/V 'Romuald Muklevich', sta. 61, 69°00.380′N, 40°02.650′E	ZMMU Op-296					3 spcs	135–137	22.viii.2003	P.A. Lyubin
D. robustus	Barents Sea, R/V 'Romuald Muklevich', sta. 48, 69°32.371′N, 38°32.880′E	ZMMU Op-342					2 spcs	101–110	19.viii.2003	P.A. Lyubin
D. robustus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-343	KM397002	KM397084	KM397106	KM397043	2 spcs	5–10	15.viii.2012	T.A. Korshunova, A.V. Martynov
D. robustus	Barents Sea, Dalne-Zeleneckaya Bay	ZMMU Op-344	KM397003	KM397085	KM397107	KM397044	2 spcs	5–10	15.viii.2012	T.A. Korshunova, A.V. Martynov
D. robustus	White Sea	ZMMU Op-345					1 spc.	20	vii.2001	–
D. robustus	Bering Strait, R/V 'Healy', sta. 96, 63°973.766′N; 173°061.99′E	ZMMU Op-346					3 spcs	67	30.v.2006	B.I. Sirenko
D. robustus	Bering Strait, R/V 'Healy', sta. 26, 63°106.302′N; 173°088.25′E	ZMMU Op-360					2 spcs	72	16.v.2006	B.I. Sirenko
D. robustus	Bering Strait, R/V 'Healy', sta. 41, 63°035.11′N; 173°455.58′E	ZMMU Op-348					1 spc.	64	20.v.2006	B.I. Sirenko
D. robustus	Kara Sea, R/V 'Dalnie Zelentsy', sta. 2vp-37, 73°48.6′N, 75°35.1′E	ZMMU Op-348					1 spc.	21	13.ix.2012	O.L. Zimina
D. robustus	Barents Sea, R/V 'Dalnie Zelentsy', sta. MB-2, 68°56.9′N, 57°56.9′E	ZMMU Op-390	KM396963 KM396964 KM396965 KM396966 KM396968	KM397045 KM397046 KM397047 KM397048 KM397051	KM397115 KM397116 KM397117 KM397118 KM397119	KM397004 KM397005 KM397006 KM397007 KM397009	8 spcs	13	22.vii.2013	O.L. Zimina
D. robustus	Barents Sea, R/V 'Dalnie Zelentsy', sta. MB-5, 69°07.8′N, 58°05.5′E	ZMMU Op-391	KM396970	KM397053	KM397120	KM397011	3 spcs	18	19.vii.2013	O.L. Zimina
D. robustus	Barents Sea, R/V 'Dalnie Zelentsy', sta. MB-13, 69°14.8′N, 57°59.6′E	ZMMU Op-392	KM396967	KM397049	KM397121	KM397008	6 spcs	19	19.vii.2013	O.L. Zimina
D. robustus	Barents Sea, R/V 'Dalnie Zelentsy', sta. MB-14, 69°08.3′N, 57°48.0′E	ZMMU Op-393	KM396969	KM397052	KM397122	KM397010	1 spc.	17	18.vii.2013	O.L. Zimina
D. robustus	Barents Sea, R/V 'Dalnie Zelentsy', sta. CB-23, 75°01.6′N, 38° 00.9′E	ZMMU Op-395					1 spc.	182–184	11.vi.2013	O.L. Zimina
D. robustus	Barents Sea, R/V 'Dalnie Zelentsy', sta. CB-17, 75°14.4′N, 39°45.4′E	ZMMU Op-396					1 spc.	234–237	11.vi.2013	O.L. Zimina

Pacific coast of Kamchatka and from the Bering Strait, specimens of *D. niveus* sp. nov. were collected from the White and the Barents seas, including the Spitsbergen area, specimens of *D. frondosus* were collected from Norway, and from the White and the Barents seas, specimens of *D. robustus* were collected from the Bering Strait, and the White, the Barents, and the Kara seas, and specimens of *D. lacteus* were collected from Norway and the Barents Sea, including the Spitsbergen area and Franz Josef Land.

Morphological analysis

The external morphology of molluscs was studied under a stereomicroscope. For the description of internal features we dissected both preserved and fresh specimens (when available) under the stereomicroscope. The buccal mass of each specimen was extracted and soaked in 10% sodium hypochlorite solution for 1–2 minutes to dissolve connective and muscle tissue, leaving only the radula and the jaws. The features of the jaws of each species were analysed under the stereomicroscope and scanning electron microscope, and then drawn. The coated radulae were examined and photographed using a scanning electron microscope (CamScan, JEOL JSM). The reproductive systems of different species were also examined and drawn using the stereomicroscope.

Molecular analysis

Taxon sampling

For phylogenetic reconstruction we used 56 individuals belonging to the various species of the genus *Dendronotus*. Specimens from different localities and/or with differing patterns of coloration were chosen and preserved in 70–96% ethanol. Previously published sequences of several *Dendronotus* species that had already been retrieved from GenBank were also used to place the new species in a phylogenetic framework (Table S1). Specimens of Scyllaeidae and Dotoidae, as well as specimens of the genera *Tritonia* and *Janolus*, were included in the analysis to test the monophyly of Dendronotidae. These out-group taxa were chosen based on the results of Stout *et al*. (2010) and Pola & Gosliner (2010).

DNA extraction, amplification, and sequencing

DNA was extracted from the small pieces of foot tissue for all available specimens (see Table 1) preserved in 70–96% ethanol using either the Diatom™ DNA Prep 100 kit by Isogene Lab or the Wizard® SV Genomic DNA purification kit by Promega, according to the manufacturers' protocols. Extracted DNA was used as a template for the amplification of partial sequences of the mitochondrial genes cytochrome *c* oxidase subunit I (*COI*) and *16S* rRNA, and the nuclear genes *Histone 3* (*H3*) and *28S* rRNA (C1–C2 domain). The primers that were used for amplification are shown in Table 2. Polymerase chain reaction (PCR) amplifications were carried out in a 20-μL reaction volume, which included 4 μL of 5x Screen Mix by Eurogen Lab, 0.5 μL of each primer (10 μM stock), 1 μL of genomic DNA, and 14 μL of sterile water. The amplification of *COI* and *28S* was performed with an initial denaturation for 1 min at 95 °C, followed by 35 cycles of 15 s at 95 °C (denaturation), 15 s at 45 °C (annealing temperature), and 30 s at 72 °C, with a final extension of 7 min at 72 °C. The amplification of *H3* began with an initial denaturation for 1 min at 95 °C, followed by 40 cycles of 15 s at 95 °C (denaturation), 15 s at 50 °C (annealing temperature), and 30 s at 72 °C, with a final extension of 7 min at 72 °C. The *16S* amplification began with an initial denaturation for 1 min at 95 °C, followed by 40 cycles of 15 s at 95 °C (denaturation), 15 s at 52 °C (annealing temperature), and 30 s at 72 °C, with a final extension of 7 min at 72 °C. Sequencing

Table 2. Polymerase chain reaction (PCR) and sequencing primers

Name	5′→3′	References
Onu_16S_F1_M13	TGTAAAACGACGGCCAGTCTGTTTAMCAAAAACATHGCCT	Budaeva *et al*., unpublished
Onu_16S_R1_M13	CAGGAAACAGCTATGACGCTTACGCCGGTCTGAACTCAG	Budaeva *et al*., unpublished
16S arL	CGCCTGTTTAACAAAAACAT	Palumbi *et al*. (2002)
16S R	CCGRTYTGAACTCAGCTCACG	Puslednik & Serb, 2008
LCO 1490	GGTCAACAAATCATAAAGATATTGG	Folmer *et al*., 1994
HCO 2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer *et al*., 1994
28S C1′	ACCCGCTGAATTTAAGCAT	Lê *et al*., 1993
28S C2	TGAACTCTCTCTTCAAAGTTCTTTTC	Lê *et al*., 1993
H3 AF	ATGGCTCGTACCAAGCAGACGG	Colgan *et al*., 1998
H3 AR	ATATCCTTGGGCATGATGGTGAC	Colgan *et al*., 1998
M13F	GTTGTAAAACGACGGCCAGT	
M13R	CACAGGAAACAGCTATGACC	

for both strands proceeded with the Big Dye v3.1 sequencing kit from Applied Biosystems. The same primers as used for PCR were used for all genes, except where M13 universal sequencing primers were used. Sequencing reactions were analysed using an ABI 3500 Genetic Analyser by Applied Biosystems at the N.K. Koltsov Institute of Developmental Biology (Moscow, Russia) and also with an ABI 3500 Genetic Analyser from Applied Biosystems at N.A. Pertsov White Sea Biological Station of the Moscow State University (Russia). All new sequences were deposited in GenBank.

Sequence analysis

Raw reads for each gene were assembled and checked for improper base-calling using CodonCode Aligner 2.0.6 (Codon Code Corporation). Original data and publicly available sequences were aligned with the MUSCLE (Edgar, 2004) algorithm in MEGA 5 (Tamura *et al*., 2011). Protein-coding sequences were translated into amino acids for confirmation of the alignment. The resulting alignments were of 645 bp for *COI*, 329 bp for *H3*, 467 bp for *16S*, and 350 bp for *28S*. Pairwise uncorrected and corrected genetic distances were calculated for *COI* and *16S* rRNA using MEGA 5 to compare our specimens with other *Dendronotus* species. All codon positions were selected for the analysis.

Model selection and phylogenetic analysis

Individual gene analyses, separate mitochondrial and nuclear gene analyses, and a concatenated analysis were performed in this study. The best-fitting nucleotide evolution models were tested in the MEGA 5 toolkit using the Bayesian information criterion (BIC). The *28S* partition scored the lowest BIC for the Tamura three-parameter model, and *H3* and *16S* partitions scored lowest BICs for the Tamura three-parameter model with a gamma distribution of rates among sites. The best-fitting model for *COI* partition was Hasegawa–Kishino–Yano with a gamma distribution of rates among sites, with a fraction of sites being invariable. Phylogeny reconstructions of individual gene data sets were conducted by maximum-likelihood method, implemented in MEGA 5 with 2000 bootstrap pseudoreplications and in MrBayes 3.2 (Ronquist & Huelsenbeck, 2003). Reconstructions based on combined data sets (mitochondrial, nuclear, and concatenated analyses) were performed applying evolutionary models for partitions separately. Bayesian estimation of posterior probability was also performed in MrBayes 3.2. Markov chains were sampled at intervals of 500 generations. Analysis was started with random starting trees and 5×10^6 generations. Maximum likelihood-based phylogeny inference for all combined data sets was performed in GARLI 2.0 (Zwickl, 2006) with bootstrap in 1000 pseudoreplications. Bootstrap values were placed on the best tree found with SumTrees 3.3.1 from DendroPy Phylogenetic Computing Library 3.12.0 (Sukumaran & Holder, 2010). Final phylogenetic tree images were rendered in FigTree 1.4.0.

Species delimitation

We used two methods to define species: comparing single- and combined-gene tree topologies and Automatic Barcode Gap Discovery (ABGD). Single-gene trees were calculated using MEGA 5 and MrBayes 3.2, as described above. The ABGD method (Puillandre *et al*., 2012a) is based on pairwise distances, detecting the breaks in the distribution reffered to as the 'barcode gap' (Hebert, Ratnasingham & de Waard, 2003) without any prior species hypothesis. It is commonly used for species delimitation analyses, including the latest works on opisthobranch taxa (Jörger *et al*., 2012; Barco *et al*., 2013; Krug *et al*., 2013; Cámara *et al*., 2014; Carmona *et al*., 2014; Churchill, Valdés & Foighil, 2014; Ortigosa *et al*., 2014; and others). The ABGD program is available from http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html. We analysed *COI* and *16S* FASTA alignments separately (excluding out-groups) using both proposed models: Jukes-Cantor (JK69) and Kimura (K80). In the case of *COI*, P_{max} was increased to 0.20 and the number of steps was increased to 15. Other settings remained as the default settings. In *16S* analysis the default settings were used.

RESULTS

SYSTEMATIC DESCRIPTIONS

DENDRONOTUS FRONDOSUS (ASCANIUS, 1774)

FIGURES 1, 2, 3, 4, 5, 6A, 7A, 8A

Amphitrite frondosa Ascanius, 1774: 155–158, pl. 5, fig. 2.

Dendronotus frondosus – Mörch, 1871: 182; Norman, 1890: 78–79; Robilliard, 1970: 441–446, pl. 63, fig. 29, text and figs 4, 7, 8, 9 (partim); McDonald, 1983: 173–176 (partim); Deryugin, 1928: 319–320; Roginskaya, 1962: 88, 93–95, 106, fig. 2(1–3); Roginskaya, 1987: 173–175, fig. 105 (partim); Evertsen & Bakken, 2005: 18; Martynov *et al*., 2006: 63 (partim).

Doris arborescens Müller, 1776: 229.

Tritonia arborescens – Cuvier, 1805: 435, pl. 61, figs 8–10.

Dendronotus arborescens – Alder & Hancock, 1845–1855: fam. 3, pl. 3, pt 1; Wagner, 1885: 58; Guryanova, 1924: 160; Filatova, Zatsepin, 1948: 399, pl. 102, fig. 1.

Doris cervina Gmelin, 1791: 3105, no. 12.

?Tritonia reynoldsii Couthouy, 1838: 74–80, pl. 2, figs 1–4.

Tritonia felina Alder & Hancock, 1842: 33.

Tritonia pulchella Alder & Hancock, 1842: 33.

Tritonia ascanii Møller, 1842: 78.

Amphitridea fabricii Kröyer, 1847: 114.

Figure 1. *Dendronotus frondosus* (Ascanius, 1774). Living animal. Neotype ZMMU Op-380. Norway, entrance of the Sognefjord, Gulen Dive Resort, 32 mm in length. A, dorsal view; B, ventral view; C, lateral view; D, dorsolateral appendages. Photos by T.A. Korshunova.

Campaspe pusilla Bergh, 1863: 471–478, pl. 12, figs 28–35.

Campaspe major Bergh, 1886: 21–24, pl. 1, figs 23–26, pl. 2, figs 1–11.

Non *Dendronotus frondosus sensu* Ushakov, 1953: 258; Volodchenko, 1955: 248, pl. 48, fig. 1; Roginskaya, 1998: 51–53; Martynov, 1997: 78.

Type material

Unknown, probably lost (K. Kvalsvik, Zoological Museum, University of Oslo, pers. comm.). Neotype is designated here (ZMMU Op-380, one spec., Norway, entrance of the Sognefjord, Gulen Dive Resort, 5–10 m depth, 18.iii.2014, coll. T.A. Korshunova, A.V. Martynov).

Material examined

ZMMU Op-324, seven spcs, L = 7–10 mm (live), two dissected, Barents Sea, Dalne-Zelenetskaya Bay, 0.3–0.4 m depth, 5.viii.2005, coll. A.V. Martynov, T.A. Korshunova. ZMMU Op-325, eight spcs, L = 6–12 mm (live), three dissected, Barents Sea, Dalne-Zelenetskaya Bay, 0.5–0.6 m depth, 4.viii.2005, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-326, eight spcs, L = 5–10 mm, two dissected, Barents Sea, Plokhie Chevry Bay, 0.3–0.4 m depth, 6.viii.2005, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-327, six spcs, three dissected, Barents Sea, Plokhie Chevry Bay, 1 m depth, 15.viii.2005, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-319, ten spcs, L = 8–

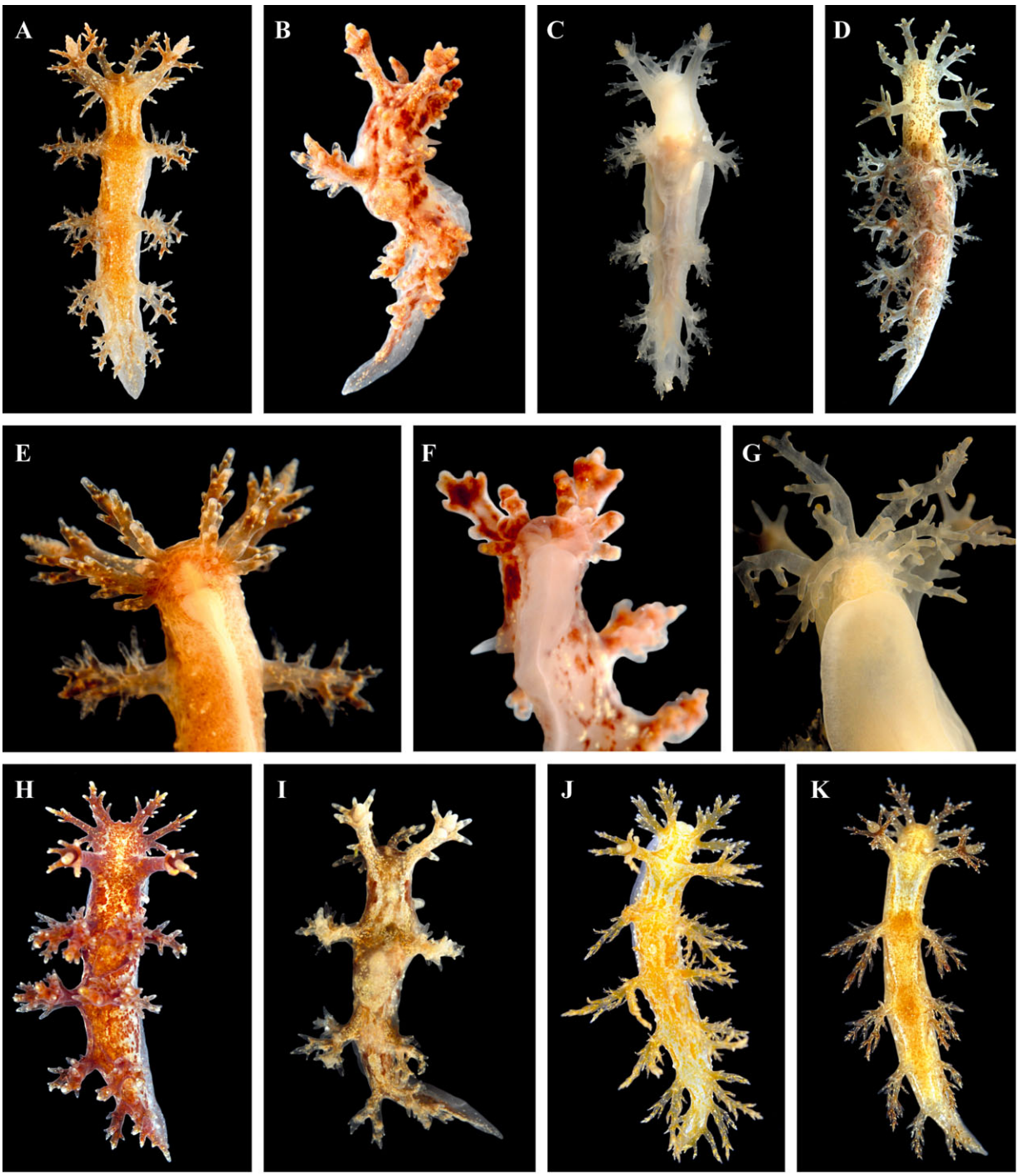

Figure 2. *Dendronotus frondosus* (Ascanius, 1774). Living animals. Different patterns of coloration. A, Barents Sea, Dalne-Zeleneckaya Bay, 14 mm in length, photo by T.A. Korshunova, ZMMU Op-297. B, Barents Sea, Dalne-Zeleneckaya Bay, 8 mm in length, photo by T.A. Korshunova, ZMMU Op-312. C, Barents Sea, Dalne-Zelelneckaya Bay, 17 mm in length, photo by T.A. Korshunova, ZMMU Op-300. D, Barents Sea, Dalne-Zelelneckaya Bay, 11 mm in length, photo by T.A. Korshunova. E, Barents Sea, Dalne-Zeleneckaya Bay, 14 mm in length, photo by T.A. Korshunova, ZMMU Op-297. F, Barents Sea, Dalne-Zeleneckaya Bay, 8 mm in length, photo by T.A. Korshunova, ZMMU Op-312. G, Barents Sea, Dalne-Zelelneckaya Bay, 17 mm in length, photo by T.A. Korshunova, ZMMU Op-300. H, Barents Sea, Varangerfjord, 23 mm in length, photo by T.I. Antohina, ZMMU Op-315. I, Barents Sea, Dalne-Zeleneckaya Bay, 12 mm in length, photo by T.A. Korshunova, ZMMU Op-304. J, Barents Sea, Varangerfjord, 22 mm in length, photo by T.I. Antokhina, ZMMU Op-316; K, Barents Sea, Varangerfjord, 18 mm in length, photo by T.I. Antokhina, ZMMU Op-315.

Figure 3. *Dendronotus frondosus* (Ascanius, 1774). Living animals. Different patterns of coloration. A, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 12 mm in length, photo by A.A. Semenov. B, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 15 mm in length, photo by A.A. Semenov. C, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 17 mm in length, photo by A.A. Semenov. D, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 16 mm in length, photo by A.A. Semenov. E, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 11 mm in length, photo by A.A. Semenov. F, Barents Sea, Dalne-Zeleneckaya Bay, photo by O.V. Savinkin.

15 mm (live), one dissected, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 10–12 m depth, 25.iv.2007, coll. N.A. Chervyakova. ZMMU Op-322, five spcs, *L* = 5–10 mm, two dissected, White Sea, Kandalaksha Bay, Kartesh, 0.2–0.6 m depth, 5.vi.2008, coll. A.V. Martynov, T.A. Korshunova. ZMMU Op-291, four spcs, three dissected, Barents Sea, Dalne-Zelenetskaya Bay, 0.1–0.2 m depth, vii.2008, coll. A.V. Martynov, T.A. Korshunova. ZMMU Op-328, three spcs, all dissected, Barents Sea, Dalne-Zelenetskaya Bay, 2–5 m depth, 12.viii.2006, coll. A.V. Martynov, T.A. Korshunova. ZMMU Op-292, five spcs, four dissected, Barents Sea, Plokhie Chevry Bay, 0.5–0.7 m depth, 23.viii.2006, coll. A.V. Martynov, T.A. Korshunova. ZMMU Op-323, five spcs, *L* = 8–12 mm, three dissected, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 7–10 m depth, 3.vi.2009, coll. A.V. Martynov, T.A. Korshunova. ZMMU Op-318, five spcs, *L* = 8–14 mm (live), two dissected, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 0.3 m depth, 12.ix.2011, coll. I.A. Ekimova. ZMMU Op-317, three spcs, *L* = 6–11 mm (live), two dissected, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 0.1–0.2 m depth, 13.ix.2011, coll. I.A. Ekimova. ZMMU Op-293, four spcs, *L* = 7–14 mm (live), White Sea, Kandalaksha Bay, Velikaya Salma Strait, 0.1–0.2 m depth, 13.ix.2011, coll. I.A. Ekimova. ZMMU Op-320, seven spcs, *L* = 10–16 mm (live), all dissected, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 7–10 m depth, 14.ix.2011, coll. A.A. Semenov. ZMMU Op-321, six spcs, *L* = 12–15 mm (live), three dissected, White

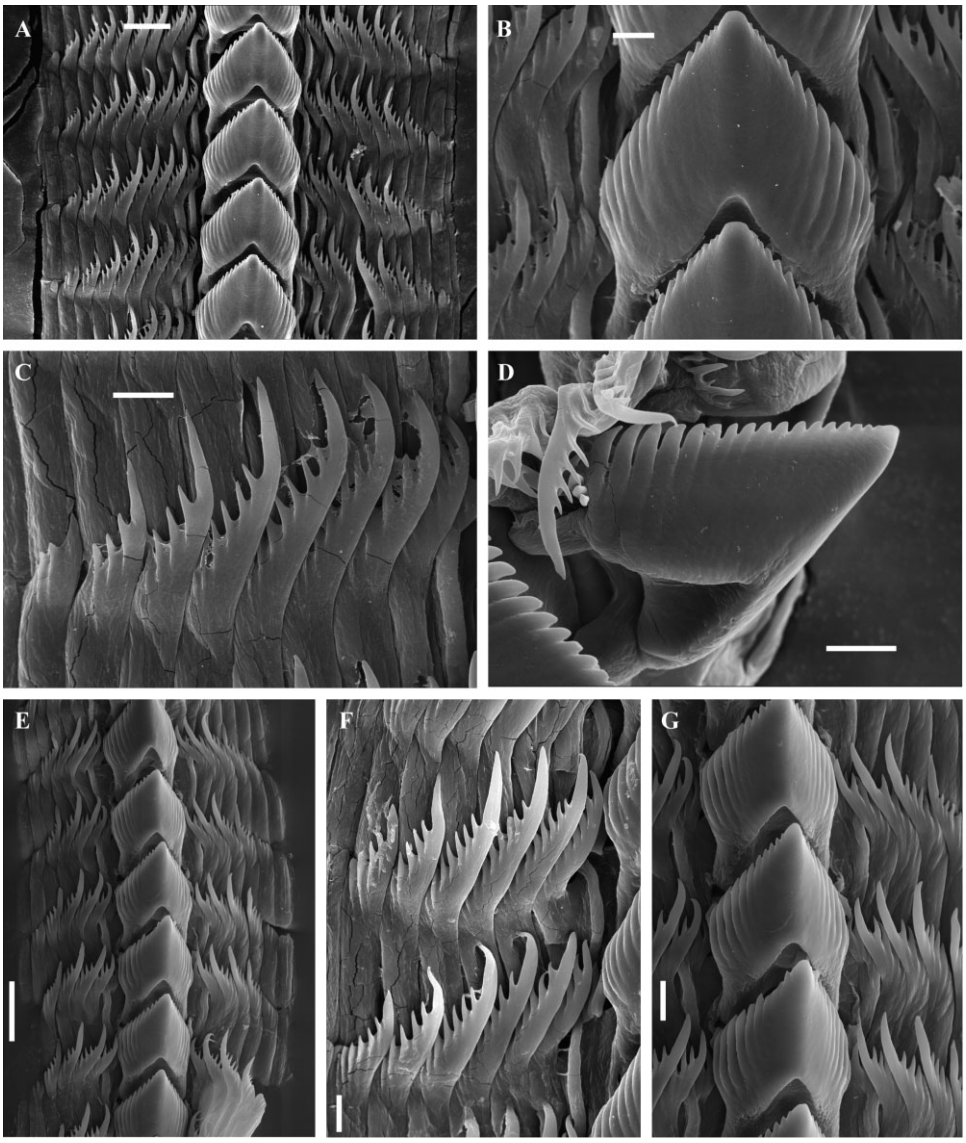

Figure 4. *Dendronotus frondosus* (Ascanius, 1774). Scanning electron micrographs of the radula. A, ZMMU Op-320, specimen 14 mm in length, rachidian and lateral teeth, scale bar = 30 μm. B, ZMMU Op-320, specimen 14 mm in length, rachidian tooth, scale bar = 10 μm. C, ZMMU Op-320, specimen 14 mm in length, lateral teeth, scale bar = 10 μm. D, ZMMU Op-293, specimen 14 mm in length, rachidian tooth, scale bar = 10 μm. E, ZMMU, D-326 specimen 12 mm in length, rachidian and lateral teeth, scale bar = 10 μm. F, ZMMU Op-326, specimen 12 mm in length, lateral teeth, scale bar = 10 μm. G, ZMMU Op-326, specimen 12 mm in length, rachidian teeth, scale bar = 10 μm.

Sea, Kandalaksha Bay, Velikaya Salma Strait, 10 m depth, 17.ix.2011, coll. A.A. Semenov. ZMMU Op-290, ten spcs, *L* = 14–20 mm (live), White Sea, Kandalaksha Bay, Velikaya Salma Strait, 0.1–0.2 m depth, 2.vii.2012, coll. I.A. Ekimova. ZMMU Op-297, 12 spcs, Barents Sea, Dalne-Zelenetskaya Bay, 0.2–0.3 m depth, 16.viii.2012, coll. A.V. Martynov, T.A. Korshunova. ZMMU Op-298, four spcs, Barents Sea, Dalne-Zelenetskaya Bay, 10 m depth, 9.viii.2012. ZMMU Op-299, nine spcs, Barents Sea, Dalne-Zelenetskaya Bay, 0.4 m depth, 3.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-300, two spcs, Barents Sea, Dalne-Zelenetskaya Bay, 0.4 m depth, 20.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-301, 11 spcs, Barents Sea, Dalne-Zelenetskaya Bay, 0.5 m depth, 2.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-302, seven spcs, Barents Sea, Dalne-Zelenetskaya Bay, 0.2–0.4 m depth, 5.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-303, seven spcs, Barents Sea, Dalne-Zelenetskaya Bay, 0.4–0.8 m depth, 17.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-304, nine spcs, Barents Sea, Dalne-Zelenetskaya Bay, 0.5 m

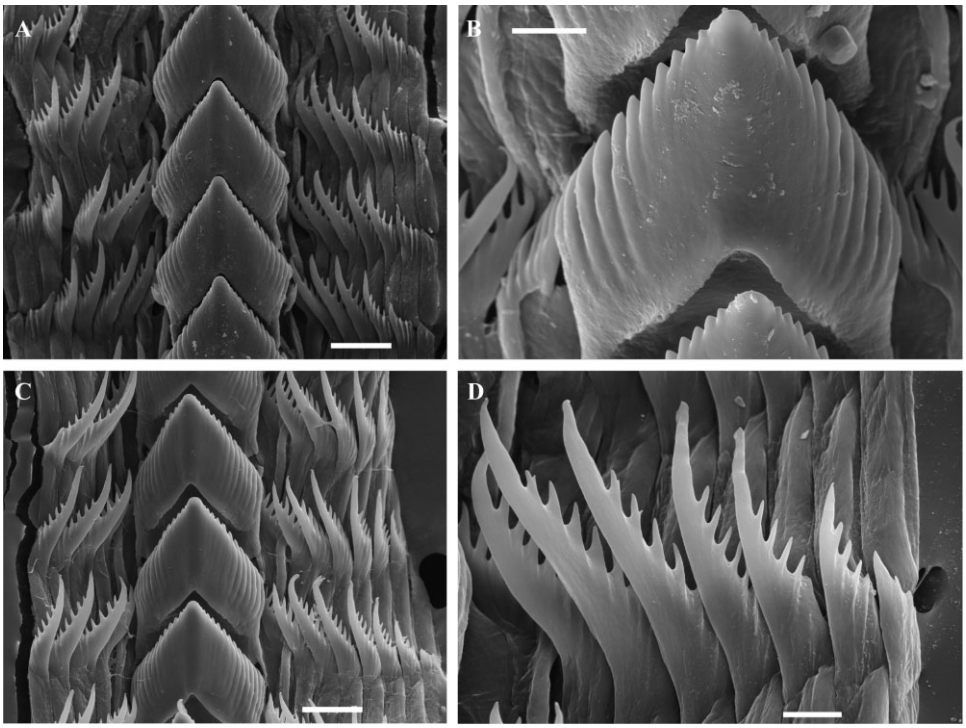

Figure 5. *Dendronotus frondosus* (Ascanius, 1774). Scanning electron micrographs of the radula. A, ZMMU Op-315, specimen 20 mm in length, rachidian and inner lateral teeth, scale bar = 30 μm. B, ZMMU Op-328, specimen 21 mm in length, rachidian tooth, scale bar = 10 μm. C, ZMMU Op-328, specimen 21 mm in length, rachidian and lateral teeth, scale bar = 30 μm. D, ZMMU Op-328, specimen 21 mm in length, lateral teeth, scale bar = 10 μm.

depth, 6.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-305, one spc., Barents Sea, Dalne-Zelenetskaya Bay, 0.2 m depth, 18.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-306, one spc., Barents Sea, Dalne-Zelenetskaya Bay, 8 m depth, 24.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-307, 16 spcs, Barents Sea, Dalne-Zelenetskaya Bay, 0.2–0.4 m depth, 4.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-308, three spcs, Barents Sea, Dalne-Zelenetskaya Bay, 5 m depth, 11.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-309, two spcs, Barents Sea, Dalne-Zelenetskaya Bay, 4 m depth, 15.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-310, one spc., Barents Sea, Dalne-Zelenetskaya Bay, 5 m depth, 13.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-311, one spc., Barents Sea, Dalne-Zelenetskaya Bay, 5 m depth, 29.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-312, one spc., Barents Sea, Dalne-Zelenetskaya Bay, 0.2 m depth, 10.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-313, two spcs, Barents Sea, Dalne-Zelenetskaya Bay, 0.2–0.3 m depth, 16.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-314, one spc., Barents Sea, Dalne-Zelenetskaya Bay, 4 m depth, 8.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-315, eight spcs, L = 8–22 mm, three dissected, Barents Sea, Varangerfjord, 0.2–0.4 m depth, 6.ix.2012, coll. T.I. Antokhina. ZMMU Op-316, eight spcs, *L* = 6–15 mm, two dissected, Barents Sea, Varangerfjord, 0.2–0.5 m depth, 2.ix.2012, coll. T.I. Antokhina. ZMMU Op-359, one spc., *L* = 25 mm, Barents Sea, R/V 'Dalnie Zelentsy', sta. UR-22, 66°02′N, 57°07.1′E, 12 m depth, 7.x.2012, coll. O.L. Zimina. ZMMU Op-381, two spcs, one dissected, Barents Sea, R/V 'Dalnie Zelentsy', st. MB-15, 69°14.3′N, 57°39.5′E, 19 m depth, 18.vii.2013, coll. O.L. Zimina. ZMMU Op-282, five spcs, one dissected, Barents Sea, R/V 'Dalnie Zelentsy', st. MB-2, 69°14.3′N, 57°39.5′E, 13 m depth, 22.vii.2013, coll. O.L. Zimina.

External morphology (Figs 1, 2, 3, 8A)

Body elongate, laterally compressed. Foot narrow, tail short. Oral veil with between four and 12 short lip papillae, and between four and six large secondary branched appendages. Rhinophoral sheaths with long stalk and five crown appendages. Lateral papilla moderate in size with small secondary branches. Rhinophores with between six and 12 lamellae. Between four and six pairs of dorsolateral processes. Dorsolateral processesses moderately branched (Fig. 8A). Some secondary branches bear tertiary branches of similar size. Digestive gland diverticula penetrate dorsolateral

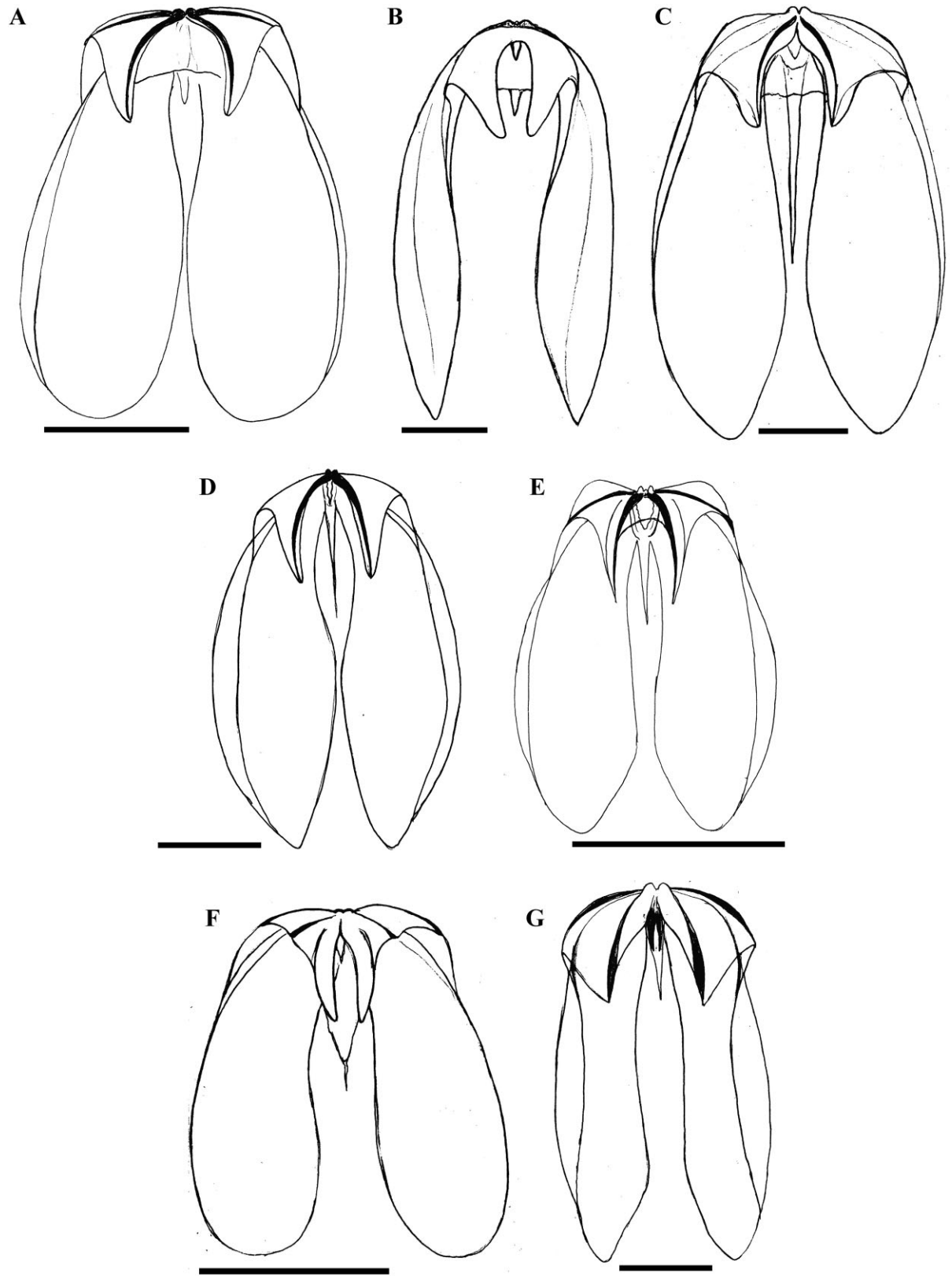

Figure 6. Jaws: A, *Dendronotus frondosus* (Ascanius, 1774); B, *Dendronotus lacteus* (Thompson, 1840); C, *Dendronotus dalli* Bergh, 1879; D, ***Dendronotus niveus* sp. nov.**; E, ***Dendronotus kamchaticus* sp. nov.**; F, ***Dendronotus kalikal* sp. nov.**; G, *Dendronotus robustus* Verrill, 1870. Scale bars: 1 mm.

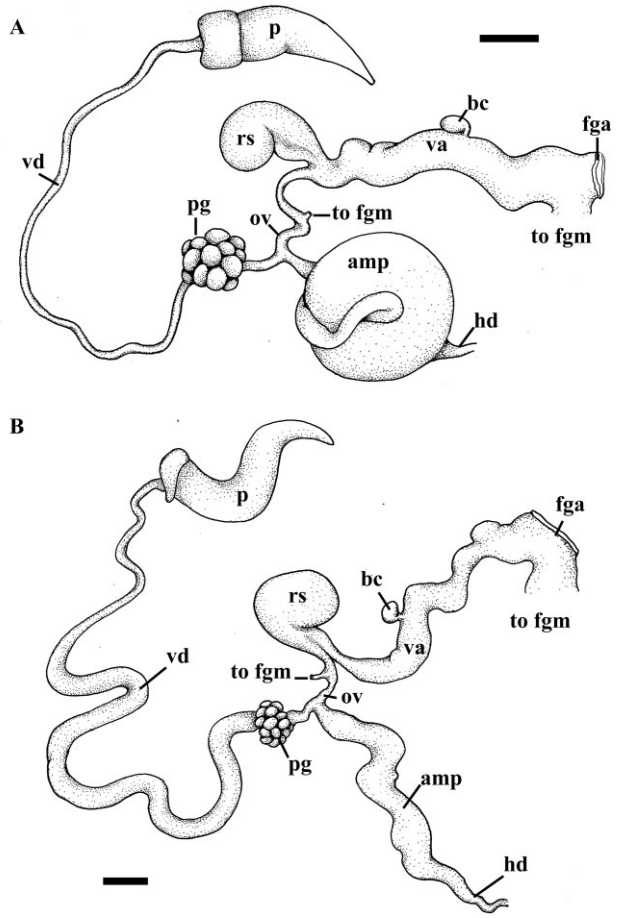

Figure 7. Reproductive system: A, *Dendronotus frondosus* (Ascanius, 1774), ZMMU Op-318; B, *Dendronotus lacteus* (Thompson, 1840), ZMMU Op-337. Abbreviations: amp, ampulla; bc, bursa copulatrix; fga, female genital aperture; fgm, female gland mass; hd, hermaphroditic duct; ov, oviduct; p, penis; pg, prostate; rs, receptaculum seminis; va, vagina; vd, vas deferens. Scale bar: 2 mm.

processes and rhinophoral branched processes. These diverticula in first pair of cerata and rhinophores originate from anterior lobe of digestive gland; others arise from posterior lobe. Anal opening on right side of body about midway between first and second pair of dorsolateral processes. Reproductive openings lateral, below first pair of dorsolateral processes on right side.

Colour (Figs 1–3)

Colour patterns vary from translucent–white (Figs 2C, G, 3C–E) specimens to reddish brown (Fig 1H). Background colour usually white or light pink. Most specimens have spots, lines, and stripes on dorsal side of the body, dorsolateral processes, rhinophoral sheaths, and upper parts of foot. In some specimens spots and lines merge between each other and form a characteristic patchy pattern. The colour of stripes and spots can vary from light (Figs 2D, J, K, 3A, B) and orange–brown (Fig. 2A, E, I) to dark, reddish brown (Fig. 2B, F) or bright red (Fig. 2H). Most specimens have opaque golden pigment on dorsal side of body, dorsolateral appendages, rhinophores, and veil papillae, which are placed in small tubercles. Purple–red specimens covered by golden pigment are also present (Fig. 3F). Digestive gland diverticula can be seen through transparent body wall. Digestive gland usually pink or brown, but some translucent–white specimens with black or green (Fig. 3C). Rhinophores similar in colour to body.

Jaws (Fig. 6A)

Length of dorsal processes of jaws about one-third length of jaw body. Inclined posteriorly at about 30°. Masticatory process about one-fifth as long as jaw body, slightly curved downwards. Masticatory border devoid of denticles. Masticatory process strong, dark at base, transparent and subulate posteriorly. Jaw body yellow, brown towards masticatory border and ligament.

Radula (Figs 4, 5)

Radula formula: 30 × 6–7.1.6–7 (ZMMU Op-321); 42 × 7–9.1.7–9 (ZMMU Op-290) 28 × 8–9.1.8–9 (ZMMU Op-291); 31 × 8–9.1.8–9 (ZMMU Op-326). Median tooth strong, triangular (Figs 4A, B, D, E, G, 5A–C), ~1.2 times longer than width. Rachidian tooth bears between ten and 12 well-defined sharp denticles with large furrows on both sides of reduced cusp. Lateral teeth (Figs 4C, E, 5D) slightly curved towards midline and possess between five and seven large sharp denticles. Outermost lateral teeth flattened with two or three reduced denticles. Innermost laterals thin with pointed apex. In juvenile specimens (L = 1–2 mm) rachidian tooth more rectangular with well-differentiated conical cusp and four or five strong denticles on both sides of cusp and large deep furrows. Only two lateral teeth in earlier juvenile specimens (L = 1–3 mm) with basal flattened plate and curved cusp bearing between two and four small denticles. In subadult specimens number of laterals increase to four or five, and become more elongate and bear between three and six denticles. Number of denticles on rachidian tooth also increases, cusp of rachidian tooth reduces, and number of denticles increases to between ten and 12 on each side.

Reproductive system (Fig. 7A)

Triaulic. Ovotestis consists of numerous white rounded lobules. Long hermafroditic duct leads to wide semicircular ampulla. Prostate discoid body consists of 16–30 small alveolar glands. Distal part of vas deferens long and winding, expanding to elongate penis. Oviduct connects through insemination duct into female gland complex. Vagina long, gradually narrowing into a rounded seminal receptaculum, and then connecting

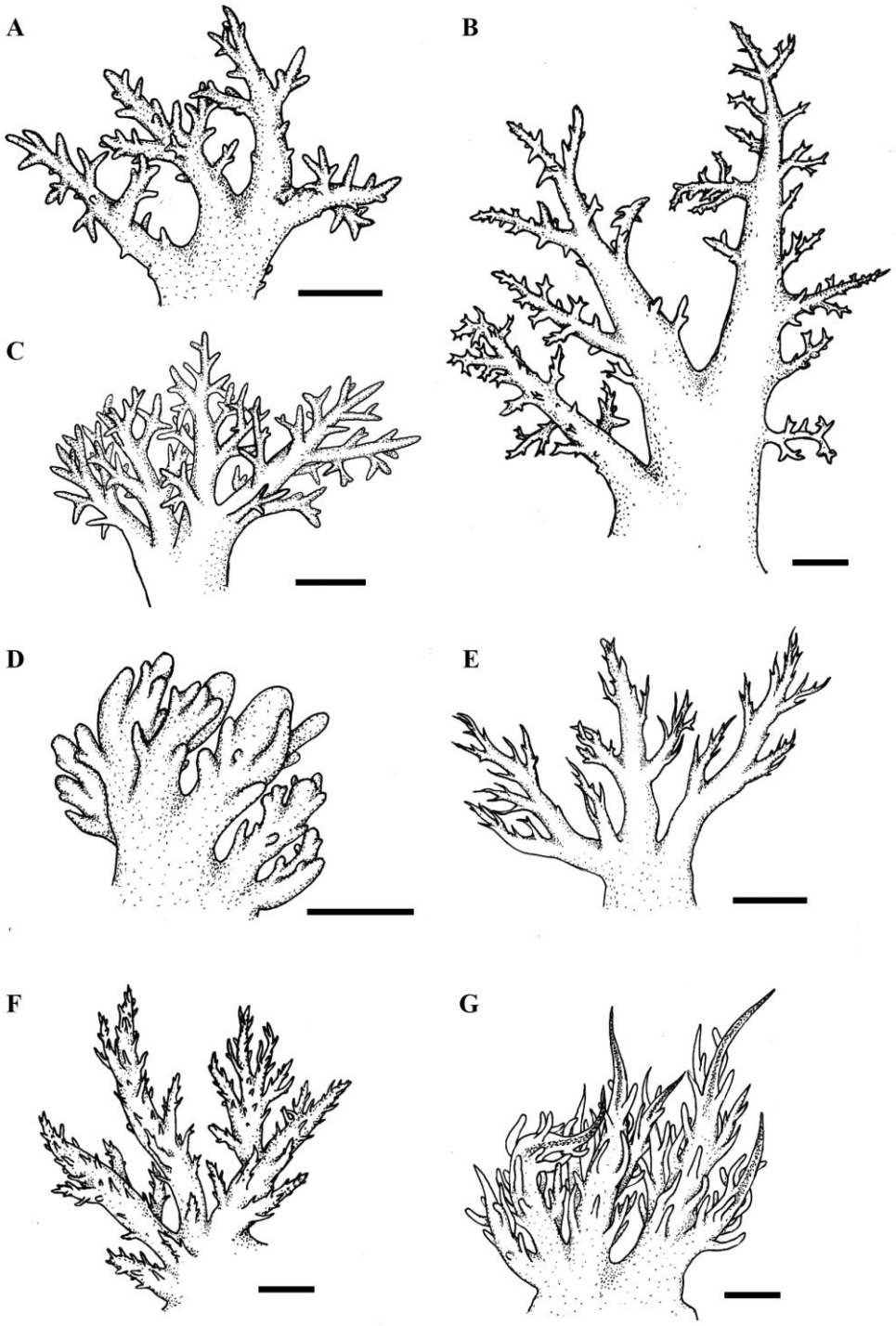

Figure 8. Dorsolateral appendage branching patterns: A, *Dendronotus frondosus* (Ascanius, 1774); B, *Dendronotus lacteus* (Thompson, 1840); C, *Dendronotus robustus* Verrill, 1870; D, ***Dendronotus kamchaticus* sp. nov.**; E, ***Dendronotus kalikal* sp. nov.**; F, ***Dendronotus niveus* sp. nov.**; G, *Dendronotus dalli* Bergh, 1879. Scale bars: 1 mm.

into oviduct and female gland mass. Bursa copulatrix small and rounded. Female genital aperture opens posterior to penis on right side of body, between first and second pairs of dorsolateral processes.

Ecology

For *D. frondosus* a wide bathymetrical range has been previously indicated (intertidal up to 400 m, Robilliard, 1970), but according to present study the

depth range does not exceed 20 m. This species is very abundant in hydrozoan associations [including *Obelia longissima* (Pallas, 1766), *Gonothyraea loveni* (Allman, 1859), and *Laomedea flexuosa* Alder, 1857] that cover various hard substrates in the White and the Barents seas, from intertidal to 10–15 m of depth. Feeds on several tecaphoran hydrozoan species from the genera *Obelia*, *Dynamena*, *Gonothyraea*, and *Laomedea*. Egg mass is narrow cord, forms an irregular, compressed off-white spiral. Reproduction period from June to October; the larva is a planctotrophic veliger with oval shell.

Distribution

North-west and north-east Atlantic, including the White and the Barents seas.

Remarks

Dendronotus frondosus shows extremely variable coloration (including white, red, and mottled specimens), but rather uniform radular morphology and shape of the dorsal appendages. Molecular analysis corroborates the morphological data (see Discussion). Two common North Atlantic species, *D. frondosus* and *D. lacteus*, may demonstrate similar colour variation, including both white and red individuals. The first description *D. frondosus* was based on the white specimens (Ascanius, 1774: 157), without morphological details. This fact was omitted in the literature, and brown-spotted specimens were commonly attributed to *D. frondosus*. As white coloration is common for *D. lacteus* it is uncertain which of the species was actually mentioned in the first description of *D. frondosus*. This may further imply considerable nomenclatural instability of the type species of the genus *Dendronotus*. In order to maintain the current usage of the specific name *D. frondosus*, we designate the neotype here (Fig. 1). The molecular data from the neotype are consistent with other specimens identified as *D. frondosus* from different localities in the North Atlantic (Stout *et al*., 2010; present study). The neotype was collected in shallow waters off the south-western coast of Norway (entrance of the Sognefjord, Gulen Dive Resort), relatively close to the type locality in the Stavanger region (Ascanius, 1774). There are a number of previous records apparently belonging to this species (reviewed e.g. in McDonald, 2009). However many of them are difficult to evaluate in the light of modern data. Presented here, synonymy is therefore restricted but still may contain records of other species. Particularly, western Atlantic *D. frondosus* (described as "*Tritonia*" *reynodlsi* Couthouy, 1838) needs to be checked for conspecificity with the European material.

DENDRONOTUS LACTEUS (THOMPSON, 1840)

FIGURES 6B, 7B, 8B, 9, 10

Tritonia lactea Thompson, 1840: 88–89, pl. 11, fig. 3; Thompson, 1856: 215, 276, 485.

Dendronotus lacteus – Pruvot-Fol, 1954: 356; Nordsieck, 1972: 68; Thollesson, 1998: 191–194, figs 1–4.

?Dendronotus luteolus LaFont, 1871: 267, pl. 17, fig. 1.

?Dendronotus arborescens var. *aurantiaca* Friele, 1879: 284.

Dendronotus velifera Pruvot-Fol, 1954: 356.

Dendronotus velifer – Nordsieck, 1972: 68 (non *Dendronotus velifer* Sars, 1878).

Dendronotus frondosus – Thompson & Brown, 1984: 22–24, text and figs 4a,b, pl. 4 d, 5c, d (partim); ?Picton & Morrow, 1994: 36.

Non *Dendronotus lacteus*: Becher, 1886: 80, pl. VI, fig. 8; Eliot 1910: 112, 161.

Non *Dendronotus lacteus*: Alder & Hancock, 1845–1855: fam. 3, pl. 3, fig. 3 (= *D. frondosus*).

Type material

Unknown.

Material examined

ZMMU Op-286, two spcs, *L* = 30–40 mm, dissected, Barents Sea, Dalne-Zelenetskaya Bay, 10–12 m depth, 23.viii.2007, coll. O.V. Savinkin. ZMMU Op-287, one spc., *L* = 35 mm, dissected, Barents Sea, Dalne-Zelenetskaya Bay, 7–10 m, 7.viii.2005, coll. O.V. Savinkin. ZMMU Op-288, one spc., *L* = 90 mm (live), dissected, Barents Sea, Dalne-Zelenetskaya Bay, 10 m depth, 6.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-289, two spcs, *L* = 20–28 mm, one dissected, Spitsbergen, 10–20 m depth, 12.viii.2009, coll. unknown. ZMMU Op-332, one spc., Barents Sea, R/V 'Johan Hjort' sta. 23, 78°09.1000′N, 14°49.4485′E, 166 m, 18.viii.2012, coll. O.S. Lyubina. ZMMU Op-333, two spcs, dissected, Barents Sea, R/V 'Johan Hjort' sta. 347, 75°06.5276′N, 21°10.3661′E, 44.7 m, 27.viii.2012 coll. O.S. Lyubina. ZMMU Op-334, one spc., Barents Sea, R/V 'Johan Hjort', sta. 451, 76°54.722′N, 22°33.279′E, 97 m, 8.ix.2012, coll. O.S. Lyubina. ZMMU Op-335, one spc., Barents Sea, R/V 'Johan Hjort', sta. 395, 76°23.225′N, 25°33.438′E, 103 m, 27.ix.2012, coll. O.S. Lyubina. ZMMU Op-336, two spcs, one dissected, Barents Sea, R/V 'Johan Hjort', sta. 342, 74°52.974′N, 16°46.176′E, 427 m, 27.viii.2012, coll. O.S. Lyubina. ZMMU Op-337, one spc., dissected, Barents Sea, Dalne-Zelenetskaya Bay, 7–10 m depth, 7.viii.2005, coll. O.V. Savinkin. ZMMU Op-338, two spcs, *L* = 15–40 mm (live), one dissected, Barents Sea, Dalne-Zelenetskaya Bay, 5 m depth, 15.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-339, one spc., Barents Sea, Dalne-Zelenetskaya Bay, 10 m depth,

Figure 9. *Dendronotus lacteus* (Thompson, 1840). Living animals. Different patterns of coloration. A, Barents Sea, Dalne-Zeleneckaya Bay, 90 mm in length, photo by T.A. Korshunova, ZMMU Op-288. B, Barents Sea, Dalne-Zeleneckaya Bay, 40 mm in length, photo by T.A. Korshunova, ZMMU Op-338. C, Barents Sea, Dalne-Zeleneckaya Bay, 90 mm in length, photo by T.A. Korshunova, ZMMU Op-288. D, Barents Sea, Dalne-Zeleneckaya Bay, 30 mm in length, photo by O.V. Savinkin, ZMMU Op-286. E, Barents Sea, Dalne-Zeleneckaya Bay, 45 mm in length, photo by O.V. Savinkin, ZMMU Op-287. F, Barents Sea, Dalne-Zeleneckaya Bay, 25 mm in length, photo by O.V. Savinkin. G, Barents Sea, Dalne-Zeleneckaya Bay, 30 mm in length, photo by O.V. Savinkin, ZMMU Op-286.

9.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-340, one spc., *L* = 25 mm, dissected, Barents Sea, R/V 'Romuald Muklevich', sta. 110, 69°00.670′N, 44°58.899′E, 58–60 m depth, 28.viii.2003, coll. P.A. Lyubin. ZMMU Op-394, one spc., dissected, Barents Sea, R/V 'Romuald Muklevich', sta. 115, 71°30.010′N, 44°58.580′E, 70 m depth, 29.viii.2003, coll. P.A. Lyubin. ZMMU Op-384, one spc., *L* = 70 mm, dissected, Franz Josef Land, Wilton Island, 80°34.6′N, 54°19.9′E, 18–28 m depth, 23.viii.2013, coll. S.D. Grebelny. ZMMU Op-385, one spc., *L* = 26 mm, dissected, Franz Josef Land, Bliss Island, 80°22.3′N, 54°39.6′E, 10–20 m depth, 24.viii.2013, coll. O.V. Savinkin. ZMMU Op-386, two spcs, *L* = 16, 35 mm, one dissected, Franz Josef Land, Pioneer Island, 80°38.198′N, 58°54.033′E, 15–23 m depth, 17.vii.2013, coll. O.V. Savinkin. ZMMU Op-387, three spcs, *L* = 30, 35, and 50 mm, Franz Josef Land, Northbrook Island, 79°56.6′N, 50°05.5′E, 18–20 m depth, 26.viii.2013, coll. S.D. Grebelny. ZMMU Op-388, three spcs, *L* = 35, 35, and 40 mm, one dissected, Franz Josef Land, Heiss Island, 80°34′N, 57°41′E, 9–25 m depth, 13.viii.2013, coll. O.V. Savinkin. ZMMU Op-389, one spc., *L* = 55 mm, dissected, Franz Josef Land, Howen Island, 81°31′N, 58°31′E, 18–31 m depth, 20.viii.2013, coll. O.V. Savinkin. ZMMU

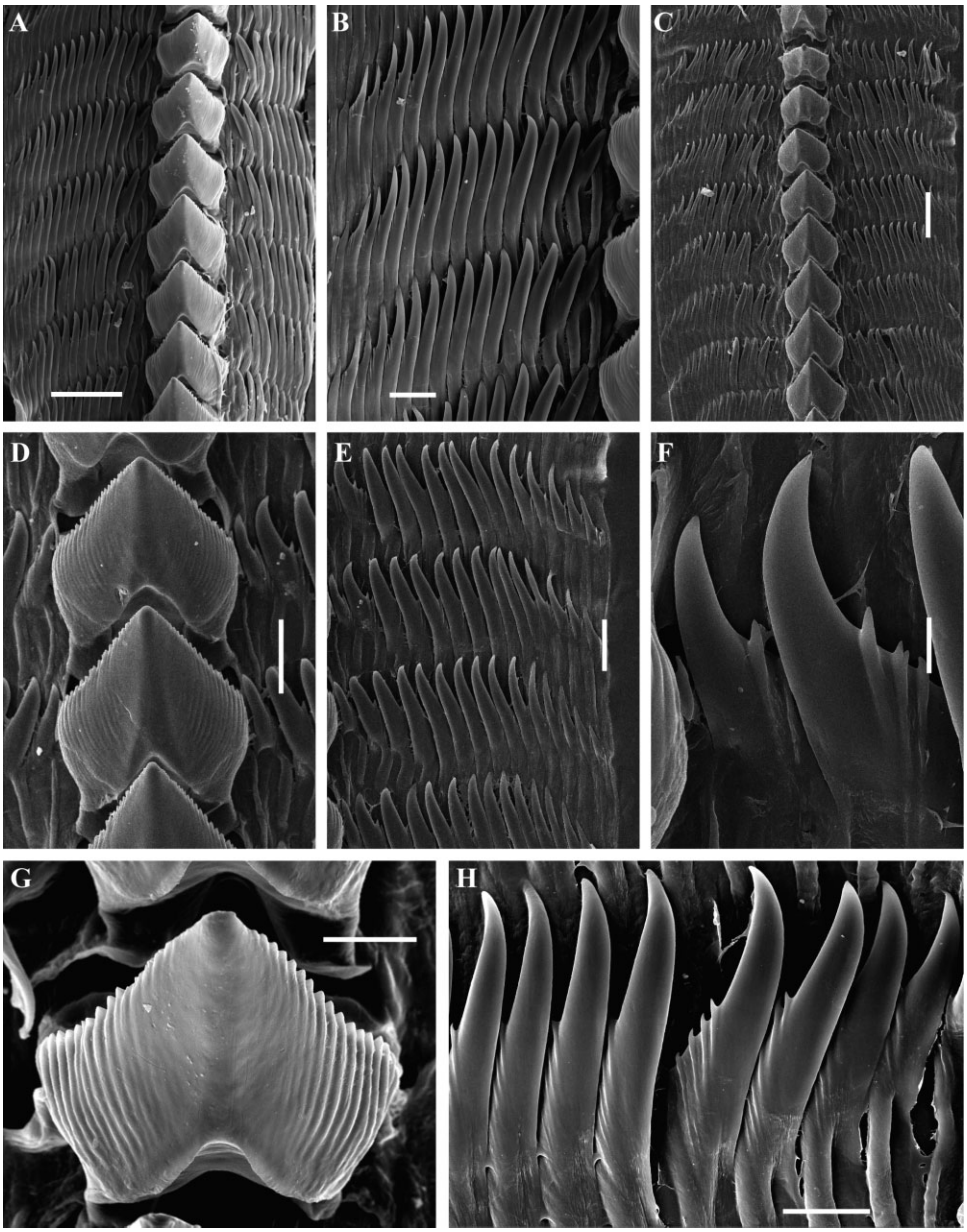

Figure 10. *Dendronotus lacteus* (Thompson, 1840). Scanning electron micrographs of the radula. A, ZMMU Op-286, specimen 45 mm in length, rachidian and lateral teeth, scale bar = 100 μm. B, ZMMU Op-286, specimen 45 mm in length, lateral teeth, scale bar = 30 μm. C, ZMMU Op-333, specimen 40 mm in length, rachidian and lateral teeth, scale bar = 70 μm. D, ZMMU Op-333 specimen 40 mm in length, rachidian teeth, scale bar = 40 μm. E, ZMMU Op-333, specimen 40 mm in length, lateral teeth, scale bar = 30 μm. F, ZMMU Op-333, specimen 40 mm in length, lateral teeth denticulation, scale bar = 10 μm. G, ZMMU Op-286, specimen 30 mm in length, rachidian tooth, scale bar = 30 μm. H, ZMMU Op-286, specimen 30 mm in length, lateral teeth denticulation, scale bar = 10 μm.

Op-383, one spc., Norway, entrance of the Sognefjord, Gulen Dive Resort, 19.iv.2014, coll. B. Picton.

External morphology (Figs 8B, 9)

Body elongate, laterally compressed. Foot narrow, tail short. Oral veil with numerous (16–24), short, lip papillae, and between five and eight large secondary branched appendages. Rhinophoral sheaths with long stalk and five or six appendages bearing secondary branches. Lateral papilla about two-thirds of sheath's length and bears small secondary branches. Rhinophores with between ten and 14 lamellae. Between five and seven pairs of dorsolateral processes. Dorsolateral appendages with very long and straight primary stalk

that branch to number of short secondary branches (Fig. 8B). Tertiary branches very short and subulate. Digestive gland diverticula penetrate to dorsolateral processes and to rhinophoral branched processes, usually not visible because of opaque coloration of body wall. Anal opening on right side of body about midway between first and second pair of dorsolateral processes. Reproductive openings placed laterally near first pair of dorsolateral processes on right side.

Colour (Fig. 9)
Common colour pattern, including body, dorsolateral processes, and rhinophoral sheath, homogeneously milky white (Fig. 9F, G). Rhinophoral lamellae yellow or orange, opaque white pigment on ceratal apices and rhinophoral sheath papillae; however, colour may vary considerably. In the North Sea and in the western part of Barents Sea (off Spitsbergen), white specimens with red stripes on dorsal side between appendages were found. In the eastern Barents Sea regions (Murman coast) brown–red specimens more often occur. They can be either homogeneous (Fig. 9D) or form striped (Fig. 9F) or spotted (Fig. 9A–C) patterns. Colour pattern also includes dots of silver or golden pigment and large white opaque spots on dorsal side of body, between dorsolateral processes. Rhinophoral lamellae brown or orange–brown.

Jaws (Fig. 6B)
Length of dorsal processes of jaws about one-third of length of jaw body; inclined posteriorly at ~30°. Masticatory process strong, dark at base, transparent, and subulate posteriorly. Masticatory border devoid of denticles. Jaw body yellow, brown towards masticatory border and ligament.

Radula (Fig. 10)
Radula formula: 40 × 10–16.1.10–16 (ZMMU Op-286); 42 × 13–15.1.13–15 (ZMMU Op-287); 42 × 12–16.1.12–16 (ZMMU Op-288); 40 × 12–15.1.12–15 (ZMMU Op-333). Rachidian tooth large and strong, triangular, wider than long, bears between 12 and 18 small denticles on both sides of reduced cusp (Fig. 10A, C, D, G). Denticles form thin furrows. Lateral teeth elongate, slightly curved, with sharp cusp (Fig. 10A–C, E). Denticles lacking or between two and five small denticles present near tooth base (Fig. 10F, H). Outer laterals thin, without denticles.

Reproductive system (Fig. 7B)
Triaulic. Ovotestis large and white, consists of number of rounded lobules. Hermaphroditic duct leads into winding ampulla. Prostate consists of more than 30 alveolar glands. Distal part of vas deferens long and winding, expands to elongate, slightly curved penis. Oviduct connects through insemination duct into female gland complex. Vagina long and convoluted, gradually narrows into rounded seminal receptaculum and then connects into oviduct and female gland mass. Bursa copulatrix small. Female genital aperture opens posterior to penis on right side of body, between first and second pairs of dorsolateral processes.

Ecology
This species was found on the hydrozoan colonies from the upper subtidal zone (10–30 m) to 427 m in depth. The previous record was also subtidal (Thollesson, 1998). Egg mass is narrow cord, forming an irregular, compressed pinkish spiral. The reproduction period is March–November, and the larva is a planctotrophic veliger with an oval shell.

Distribution
North-west Atlantic and Arctic, including Spitsbergen, Franz Josef Land, and the Barents Sea. Originally described from the UK (Irish Sea) (Thompson, 1840), it was further reliably recorded only from the Skagerrak area (Thollesson, 1998). The present data thus are a considerable extension of the range of this species to the north.

Remarks
For a long time *D. lacteus* has been considered a synonym of *D. frondosus*. Thollesson (1998) and Stout *et al*. (2010) showed a separate status of *D. lacteus*. The present study confirms these data using abundant material; however, the morphological identification of similarly coloured specimens of *D. frondosus* and *D. lacteus* is still problematic. *Dendronotus lacteus* was originally described as milky white, with occasional red or orange small dots (Thompson, 1840), but red and variegated specimens are quite common (present study). They could be easily misidentified with *D. frondosus*. The following characters can be used for distinguishing *D. frondosus* and *D. lacteus*. In *D. frondosus* secondary and tertiary branches of the dorsal processes rounded, about the same size. Lateral teeth in *D. frondosus* bear large comb-shaped denticles. In *D. lacteus* secondary branches are spiniform, considerably shorter than primary branches. The lateral teeth in *D. lacteus* bear small denticles or are completely smooth. In addition, most of the variegated specimens of *D. lacteus* specimens possess white opaque pigment on the dorsal side of the body between dorsolateral appendages. In *D. frondosus* such pigment is absent.

DENDRONOTUS DALLI BERGH, 1879
FIGURES 6C, 8G, 11, 12, 13A

Dendronotus dalli Bergh, 1879: 150; pl. 1, fig. 21; pl. 2, figs 9–12; pl. 3, figs 2–6; Robilliard, 1970: 452–455, figs 13–15; Behrens, 1980: 74; Martynov & Korshunova, 2011: 155–157.

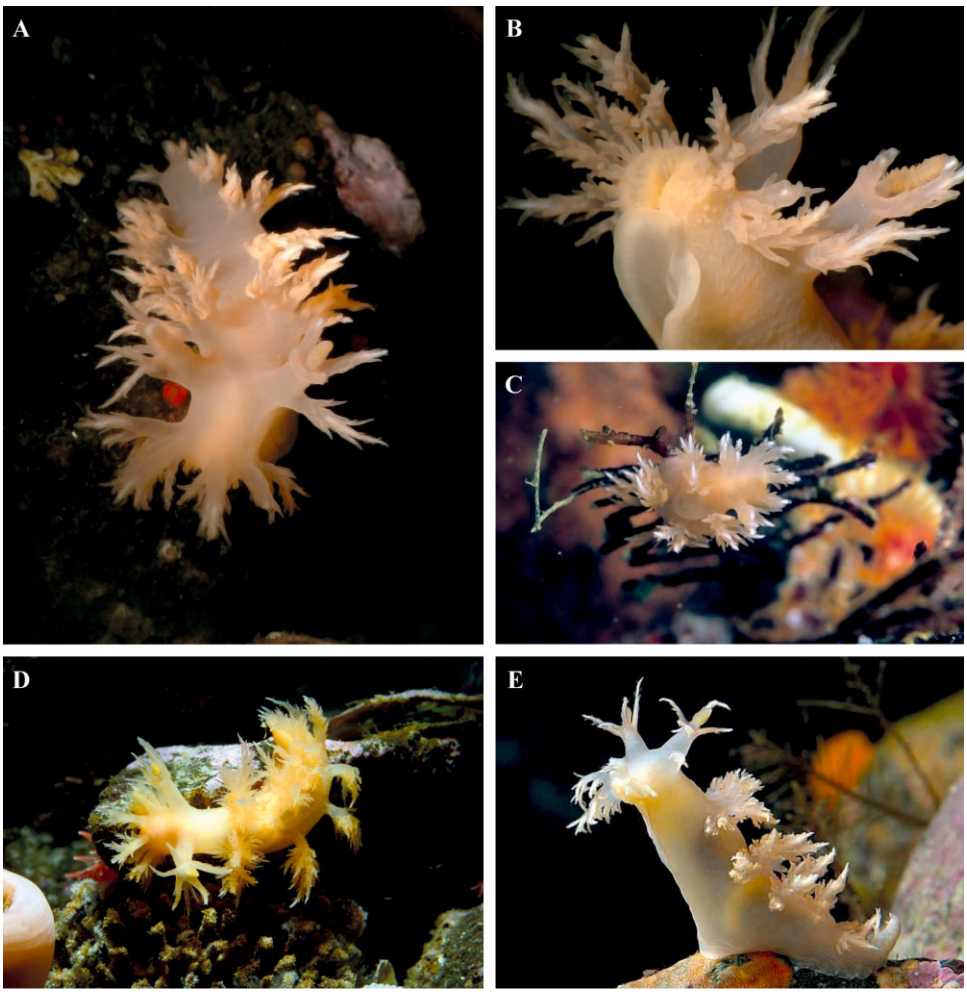

Figure 11. *Dendronotus dalli* Bergh, 1879. Living animals. A, north-west Pacific, Kamchatka, Avachinskiy Bay, 30 mm in length, photo by T.A. Korshunova, ZMMU Op-294. B, north-west Pacific, Kamchatka, Avachinskiy Bay, 30 mm in length, photo by T.A. Korshunova, ZMMU Op-294. C, north-west Pacific, Kamchatka, Avachinskiy Bay, 5 mm in length, photo by N.P. Sanamyan, ZMMU Op-331. D, north-west Pacific, Kamchatka, Avachinskiy Bay, 60 mm in length, photo by N.P. Sanamyan, ZMMU Op-330. E, north-west Pacific, Kamchatka, Avachinskiy Bay, 25 mm in length, photo by N.P. Sanamyan.

Dendronotus frondosus var. *dalli* Odhner, 1907: 64–65 (partim).

Dendronotus frondosus – Odhner, 1936: 1105–1109.

Non *Dendronotus dalli sensu* Roginskaya, 1962 (= *D. frondosus* partim).

Non *Dendronotus dalli sensu* Roginskaya, 1987 (= *D. niveus* sp. nov. partim).

Type material

Unknown, probably lost (K.R. Jensen, Zoological Museum, University of Copenhagen, pers. comm.).

Material examined

ZMMU Op-294, two spcs, L = 30–40 mm, dissected, north-west Pacific, Kamchatka, Starichkov Island, 7–12 m depth, 14.viii.2008, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-295, one spc., dissected, north-west Pacific, Kamchatka, Starichkov Island, 7–12 m depth, 19.viii.2008, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-329, two spcs, L = 6 and 28 mm, dissected, north-west Pacific, Kamchatka, Starichkov Island, 10–15 m depth, 5.x.2006, coll. N.P. Sanamyan. ZMMU Op-330, one spc., L = 10 mm, dissected, north-west Pacific, Kamchatka, Starichkov Island, 22 m depth, 15.ix.2012, coll. N.P. Sanamyan. ZMMU Op-331, one spc., L = 45 mm, dissected, north-west Pacific, Kamchatka, Starichkov Island, 22 m depth, 15.ix.2012, coll. N.P. Sanamyan.

External morphology (Figs 8G, 11)

Body elongate, laterally compressed. Foot narrow, tail short. Oral veil with 30–40 lip papillae, and between

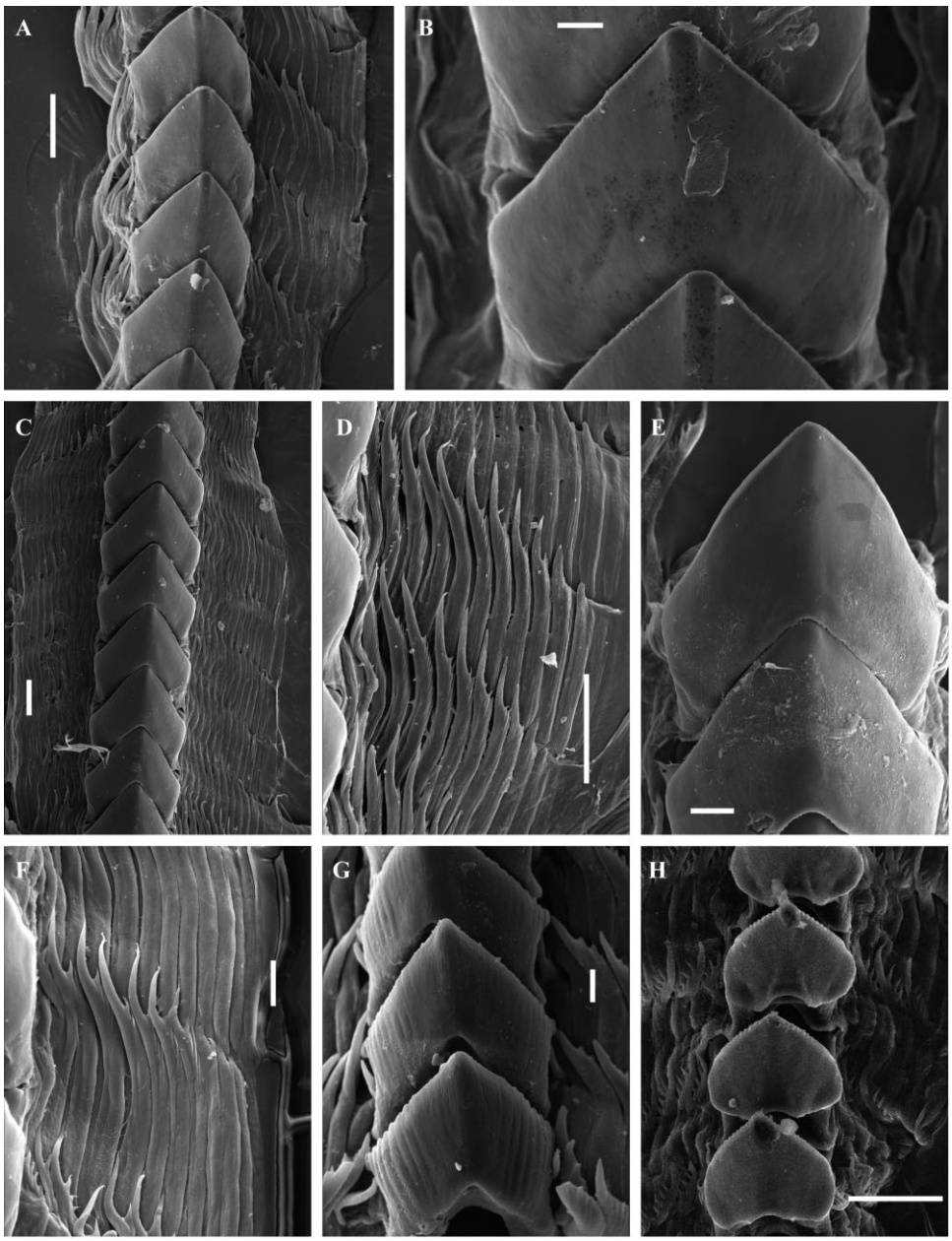

Figure 12. *Dendronotus dalli* Bergh, 1879. Scanning electron micrographs of the radula. A, ZMMU Op-351, specimen 35 mm in length, rachidian and lateral teeth, scale bar = 30 μm. B, ZMMU Op-352, specimen 40 mm in length, rachidian tooth, scale bar = 10 μm. C, ZMMU Op-330, specimen 60 mm in length, rachidian and lateral teeth, scale bar = 30 μm. D, ZMMU Op-330, specimen 60 mm in length, lateral teeth, scale bar = 30 μm. E, ZMMU Op-294, specimen 30 mm in length, rachidian tooth, scale bar = 30 μm. F, ZMMU Op-294, specimen 30 mm in length, lateral teeth, scale bar = 30 μm. G, ZMMU Op-331, specimen 7 mm in length, rachidian teeth, scale bar = 10 μm. H, ZMMU Op-329 specimen 9 mm in length, rachidian and lateral teeth, scale bar = 30 μm.

six and ten large, highly branched appendages. Rhinophoral sheaths with long stalk and five or six crown papillae, similar in size. Lateral papilla not very long, with small secondary branches. Rhinophores with 20–24 lamellae. Dorsolateral processes arranged in four to six pairs, in large specimens up to eight pairs. Dorsolateral processeses moderately branched, apices of processes smooth (Fig. 8G). Tertiary branches absent. Anal opening on right side of body about midway between first and second pair

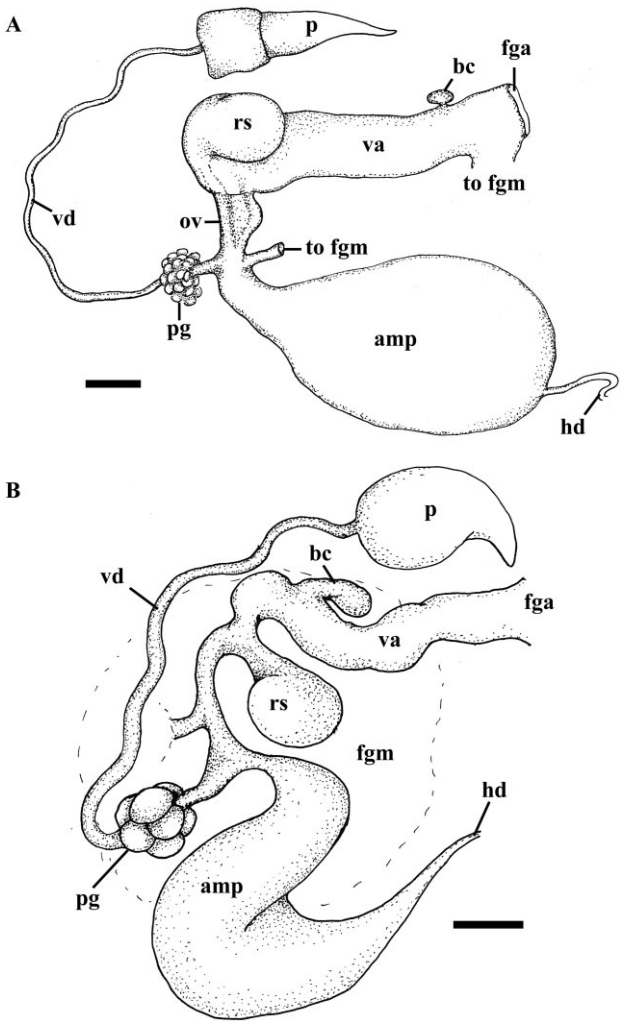

Figure 13. Reproductive system. A, *Dendronotus dalli* Bergh, 1879, ZMMU Op-294. B, ***Dendronotus niveus* sp. nov.,** ZMMU Op-275. Abbreviations: amp, ampulla; bc, bursa copulatrix; fga, female genital aperture; fgm, female gland mass; hd, hermaphroditic duct; ov, oviduct; p, penis; pg, prostate; rs, receptaculum seminis; va, vagina; vd, vas deferens. Scale bars: 2 mm.

of dorsolateral processes. Reproductive openings placed laterally near first pair of dorsolateral processes on right side.

Colour (Fig. 11)
Colour pattern uniform, varies merely from milky white to milky pink or light yellow. Apices of primary stalks covered with opaque white pigment, occuring invariably on surface of processes. Rhinophores similar in colour with body. No specimens with dark spots and stripes.

Jaws (Fig. 6C)
Length of dorsal processes of jaws is about one-quarter length of jaw body. It is inclined posteriorly at about 25°. Masticatory process about two times smaller than jaw body, dark at base, transparent and subulate posteriorly. Masticatory border has single row of rodlets.

Radula (Fig. 12)
Radula formula: 40 × 9–11.1.9–11 (ZMMU Op-294); 38 × 10–11.1.10–11 (ZMMU Op-295); 31 × 5–10.1.5–10 (ZMMU Op-331). Median tooth strong, with rectangular base and triangular cusp. Rachidian tooth of adult specimens smooth, without denticles (Fig. 12A–C, E). Laterals long and straight, with smooth cusp and three or four small denticles near their base (Fig. 12D, F). Outer teeth are thin and subulate, lacking denticles. In juvenile specimens median tooth possesses some irregular denticles with or without furrows (Fig. 12G, H).

Reproductive system (Fig. 13A)
Triaulic. Ovotestis consisting of many white rounded lobules, giving rise to long insemination duct leading to wide ampulla. Prostate consists of 30–50 alveolar glands. Distal part of vas deferens long and winding, expands to strong straight penis. Oviduct connects through insemination duct into female gland complex. Vagina long, and gradually narrows distally into rounded seminal receptaculum and connects into oviduct and female gland mass. Bursa copulatrix small and rounded. Female genital aperture opens posterior to penis on right side of body between first and second pairs of dorsolateral processes.

Ecology
This species occurs subtidally at depths of 7–100 m. Feeds on various hydrozoan colonies (Thecaphora). The reproduction period is in August–September. The egg mass is a narrow cord, forming an irregular, compressed pinkish spiral. The larva is planctotrophic veliger with oval shell.

Distribution
North-west Pacific from the North Kurile Islands to Commander Islands, Kamchatka, and the Bering Strait; north-east Pacific from Washington to Alaska.

Remarks
Specimens of *D. dalli* from the type locality (Bering Strait) were investigated for the first time. The type is unknown, but the radula of the specimens studied here is essentially similar to that illustrated in Bergh (1879). Molecular study (Fig. 24) does not reveal differences between specimens of *D. dalli* from the north-west and the north-east Pacific.

DENDRONOTUS NIVEUS SP. NOV.

FIGURES 6D, 8F, 13B, 14, 15

Dendronotus arborescens var. *dalli* Knipowitsch, 1902: 388 non Bergh, 1879.

Dendronotus dalli sensu Roginskaya, 1987 non Bergh, 1879

Type material

Holotype: ZMMU Op-269, *L* = 60 mm (live), White Sea, Kandalaksha Bay, Velikaya Salma Strait, 17 m depth, 17.ix.2012, coll. G.D. Kolbasova, A.V. Makarov.

Paratypes: ZMMU Op-270, five spcs, *L* = 9–27 mm (live), three dissected, White Sea, Kandalaksha Bay, Sidorov Island, 25 m depth, 28.vii.2012, coll. G.D. Kolbasova, N.Y. Neretin. ZMMU Op-271, one spc., 16 mm (live), dissected, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 15 m depth, 17.vii.2012, coll. G.D. Kolbasova. ZMMU Op-272, one spc., 18 mm (live), dissected, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 12 m depth, 11.vii.2012, coll. S.A. Gorin. ZMMU Op-273, three spcs, *L* = 16–20 mm, one dissected, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 17 m depth, 20.vii.2012, coll. G.D. Kolbasova. ZMMU Op-274, three spcs, *L* = 30–40 mm, dissected, Barents Sea, Bear Island, ~50 m depth, 15.v.2007, coll. R. Johansen. ZMMU Op-275, one spc., *L* = 48 mm, dissected, Barents Sea, Canin Nos Cape, R/V 'Romuald Muklevich', sta. 110, 69°00.670′N, 44°58.899′E, 58–60 m depth, 28.viii.2003, coll. Lyubin P.A. ZMMU Op-276, one spc., *L* = 37 mm, dissected, Barents Sea, R/V 'Romuald Muklevich', sta. 74, 71°00.293′N, 41°31.858′E, 85 m depth, 13.viii.2003, coll. P.A. Lyubin. ZMMU Op-277, one spc., *L* = 26 mm, Barents Sea, R/V 'Romuald Muklevich', sta. 49, 69°59.929′N, 37°59.614′E, 153–156 m depth, 19.viii.2003, coll. P.A. Lyubin. ZMMU Op-278, one spc., *L* = 32 mm, Barents Sea, R/V 'Romuald Muklevich', sta. 115, 71°30.010′N, 44°58.580′E, 70 m depth, 29.viii.2003, coll. P.A. Lyubin. ZMMU Op-279, three spcs, Barents Sea, R/V 'Johan Hjort', sta. 347, 75°06.5276′N, 21°10.3661′E, 44.7 m depth, 27.viii.2012, coll. O.S. Lyubina. ZMMU

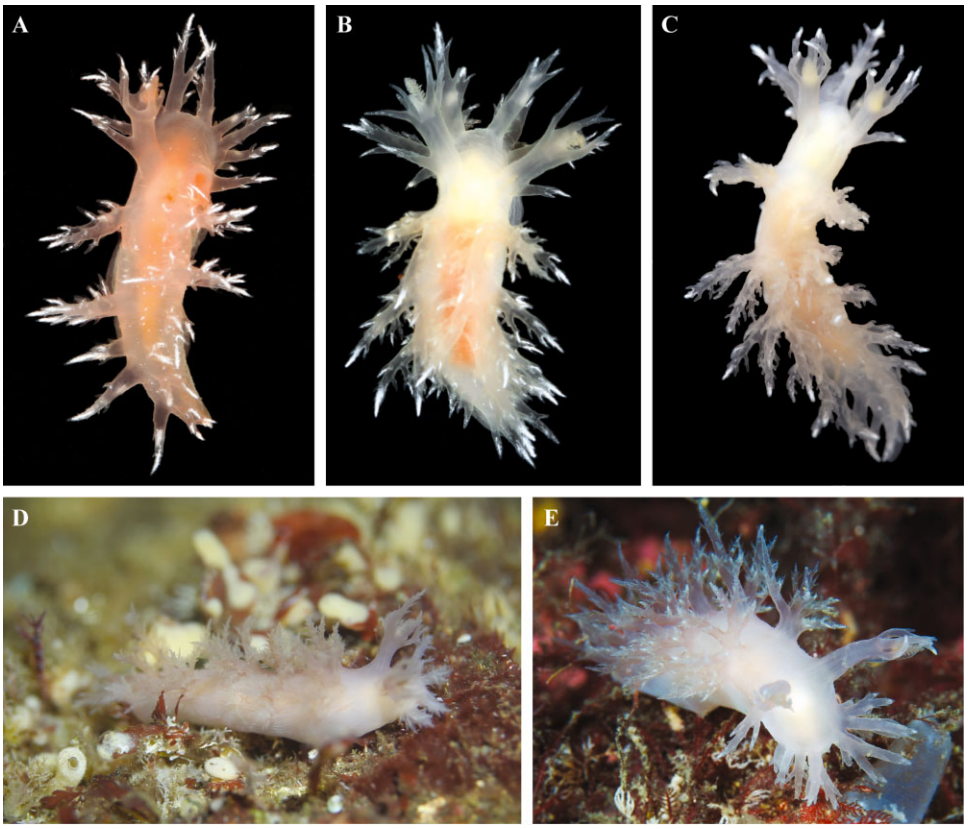

Figure 14. ***Dendronotus niveus*** **sp. nov.** Living animals. A, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 18 mm in length, photo by T.I. Antokhina, paratype ZMMU Op-270. B, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 20 mm in length, photo by T.I. Antokhina, paratype ZMMU Op-273; C, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 22 mm in length, photo by A.A. Semenov, paratype ZMMU Op-272; D, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 60 mm in length, photo by A.V. Makarov, holotype ZMMU Op-273; E, White Sea, Kandalaksha Bay, Velikaya Salma Strait, photo by A.A. Semenov.

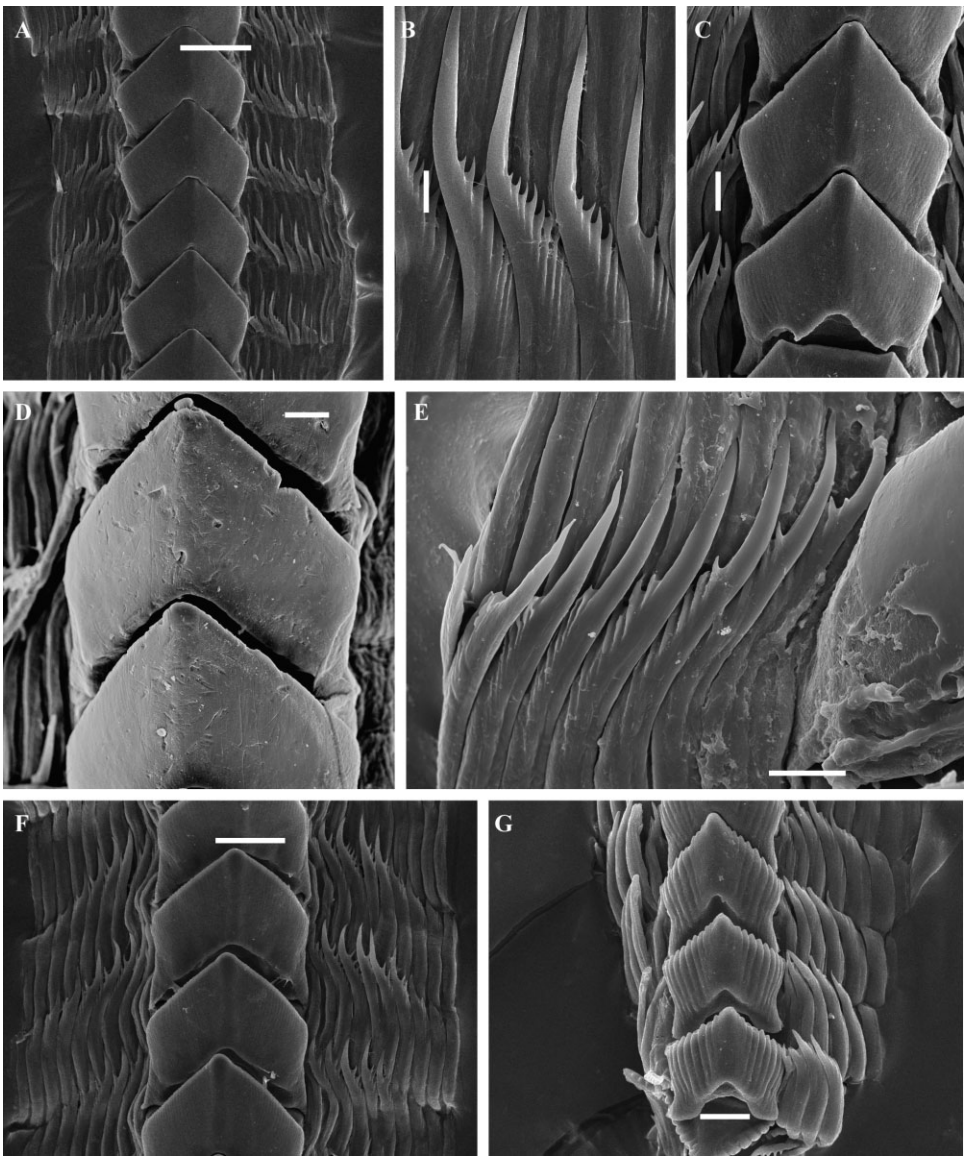

Figure 15. ***Dendronotus niveus*** **sp.nov.** Scanning electron micrographs of the radula. A, holotype ZMMU Op-269, specimen 60 mm in length, rachidian and lateral teeth, scale bar = 50 μm. B, paratype ZMMU Op-271, specimen 20 mm in length, lateral teeth, scale bar = 10 μm. C, paratype ZMMU Op-271, specimen 20 mm in length, rachidian teeth, scale bar = 20 μm. D, paratype ZMMU Op-274, specimen 45 mm in length, rachidian tooth, scale bar = 30 μm. E, paratype ZMMU Op-274, specimen 45 mm in length, lateral teeth, scale bar = 30 μm. F, paratype ZMMU Op-270, specimen 27 mm in length, rachidian and lateral teeth, scale bar = 50 μm. G, paratype ZMMU Op-270, specimen 9 mm in length, rachidian and lateral teeth, scale bar = 20 μm.

Op-280, one spc., Barents Sea, R/V 'Johan Hjort', sta. 472, 77°26.1448′N, 13°42.0457′E, 41.5 m depth, 13.ix.2012, coll. O.S. Lyubina. ZMMU Op-281, one spc., Barents Sea, R/V 'Johan Hjort', sta. 333, 75°41.3850′N, 20°49.2952′E, 42 m depth, 25.viii.2012, coll. O.S. Lyubina. ZMMU Op-282, one spc., Barents Sea, R/V 'Johan Hjort', sta. 335, 75°34.0694′N, 18°29.6825′E, 119 m depth, 25.viii.2012, coll. O.S. Lyubina. WS1102, one spc., dissected, White Sea, Kandalahsha Bay, Velikaya Salma Strait, 28 m depth, 30.vii.2011, coll. A.N. Isaychev. WS2005, one spc., White Sea, Kandalahsha Bay, Velikaya Salma Strait, 18 m depth, 22.vii.2012, coll. T.A. Antokhina. ZMMU Op-397, one spc., 75 mm in length (live), dissected, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 23 m depth, 9.vi.2014, coll. F.V. Bolshakov.

Etymology
From the Latin *niveus*, meaning snowy, snowy white refers to the most common colour pattern of this species.

External morphology (Figs 8F, 14)
Body elongate, laterally compressed. Foot narrow, tail short. Oral veil moderate, with between eight and 14 lip papillae, and between six and nine large appendages, with secondary branching. Tertiary branches absent. Rhinophoral sheaths with long stalk and five long appendages. Lateral papilla rather long, branches off sheath base, with long secondary and short tertiary branches. Rhinophores with between eight and 12 lamellae, and between five and ten pairs of dorsolateral processes. Dorsolateral processes are strongly branched with secondary branches (Fig. 8F). Longest secondary branches bear short tertiary branches. Digestive gland diverticula penetrate to dorsolateral and rhinophoral branched processes. These diverticula in first pair of cerata and rhinophores originate from anterior lobe of digestive gland; others arise from posterior lobe. Anal opening on right side of body about midway between first and second pair of dorsolateral processes. Reproductive openings placed laterally near first pair of dorsolateral processes on right side.

Colour (Fig. 14)
Body uniform, milky white, pale pink, or beige. These differences probably partially depend on food preferences. For example, specimens that were collected on *Diphasia fallax* (Johnston, 1847), with red coloration of perisarc, were pink, but after feeding on *Hydrallmania falcate* (Linnaeus, 1758), *Sertullaria mirabilis* (Verrill, 1873), and *Diphasia fallax* with white coloration in the laboratory for about a month they became paler, almost white. Brown or yellow branches of digestive gland clearly visible through semitransparent body wall in juvenile and subadult specimens. Rhinophoral lamellae same colour as body. An important characteristic of coloration is presence of opaque white pigment on ceratal apices and rhinophoral sheath. White pigment invariably placed inside appendages and shining through body wall. White pigmentation is more pronounced in juvenile and subadult specimens (Fig. 14A–C), but disappears in adults (Fig. 14D, E).

Jaws (Fig. 6D)
Length of dorsal processes of jaws about one-quarter length of jaw body. Inclined posteriorly at about 20°. Masticatory process about half jaw body length, dark at base, transparent and subulate posteriorly. Masticatory border devoid of denticles.

Radula (Fig. 15)
Radula formula: 27 × 11–13.1.11–13 (holotype ZMMU Op-269); 28 × 9.1.9 (paratype ZMMU Op-270); 26 × 9–10.1.9–10 (paratype ZMMU Op-272). Median tooth large and strong, triangular (Fig. 15A, C, D, F, G). In juvenile and subadult specimens (L = 10–15 mm) rachidian tooth bears numerous small flattened denticles (about 14–16 on each side) and shallow furrows (Fig. 15G). In adult specimens (L = 30–40 mm) denticles absent and tooth becomes completely smooth; however, furrows remain visible (Fig. 15C, F). In the largest specimens (up to 60 mm), both denticles and furrows completely absent (Fig. 5A, D). Colour of oldest median teeth brown or yellow, others transparent. Between eight and 13 lateral teeth, similar in size except for between one and three outer and one or two inner, smaller teeth with different morphology. In juvenile specimens outer teeth narrow, plate-like, and bear three or four small denticles on straight apex (Fig. 15G). In adults, outermost tooth becomes thin with pointed apex (Fig. 15B, E). Innermost lateral tooth thin, delicate, and highly denticulated. Cusps of other teeth slightly curved towards midline (about 20°), and bearing between four and eight denticles along outer border near base. Denticles small, straight, with long, thin furrows placed only in middle of tooth (i.e. about one-third of anterior part of cusp remains smooth).

Reproductive system (Fig. 13B)
Triaulic. Ovotestis light yellow, consists of number of well-defined large lobules. Hermaphroditic duct leads into large ampulla with expansion in midline. Prostate consists of between eight and ten alveolar glands. Distal part of vas deferens not very long, expanding to a slightly curved penis. Oviduct connects through insemination duct into female gland complex. Vagina long and convoluted, gradually narrows into rounded seminal receptaculum, and then connects into oviduct and female gland mass. Small bursa copulatrix near proximal part of vagina. Female genital aperture opens posterior to penis on right side of body, between first and second pairs of dorsolateral processes.

Ecology
Found subtidally at 10–120 m in depth. Feeds on various tecaphoran hydrozoan colonies (*Hydralmania* spp., *Sertullaria* spp., *Diphasia* spp., and *Sertulariella* spp.). Reproduction period in April–July. Egg mass is a narrow cord, forming an irregular, compressed pinkish spiral. Larva is planctotrophic veliger.

Distribution
Eastern North Atlantic and Arctic, including White Sea, Barents Sea, Spitsbergen, and Bear Island.

Remarks
Dendronotus niveus sp. nov. is well separated from other species of the genus *Dendronotus* according to both morphological and molecular data (Table 3; Fig. 24). Previously this species has been mentioned as

Table 3. Comparison of *Dendronotus* Alder and Hancock, 1845 species

Species	*D. albopunctatus*	*D. albus*	*D. comteti*	*D. dalli*	*D. frondosus*	*D. gracilis*	*D. iris*	***D. kalikal* sp. nov.**	***D. kamchaticus* sp. nov.**	*D. lacteus*
Distribution	San Juan Archipelago, Washington to Coos Bay, Oregon	Baja California to Alaska	Mid-Atlantic Ridge, Lucky Strike Area	North Pacific from Japan Sea and Commander Islands along Bering sea to Puget Sound, Washington	Amphi-Atlantic (north-east Atlantic, including White and Barents seas, and north-west Atlantic)	Northern Japan and New Zealand	Aleutian Islands to Baja California	North-west Pacific, Kamchatka to Bering Strait	North-west Pacific, Kamchatka	North-east Atlantic from the North and the Irish seas to the Barents Sea
Body coloration	Pale pink to dark reddish, with white spots and lines along foot margin	White to pinkish red with orange or white opaque tips on dorsolateral processes and rhinophoral sheath	Unknown (pale cream preserved)	Translucent/milky white, pale yellow, pale pink, or salmon, with white pigment on surface of dorsal processes	Variable: translucent, white, pale pink, brown, grey, yellow with brown stripes and spots, or any combination of these colour patterns	Yellow, orange, bluish white, or translucent	Red, orange, grey, with white line along foot margin	Translucent white with difficult striped pattern formed of yellow, light- and dark-brown lines, and spots	Translucent white with difficult striped pattern formed of yellow or brown lines and spots	Variable: milky white with red/brown spots and stripes, white with opaque pigment on the ends of cerata, reddish brown with golden pigment or any combinations of these patterns
Branching of dorsolateral processes	4–5 pairs, relatively few branchs; the secondary and tertiary branches, although long, are not usually extensive	4–8 pairs, strongly branched throughout all primary branches with secondary branches. The longest secondary branches bear short tertiary branches	2–4 pairs, three conical primary branches, secondary and tertiary absent	4–9 pairs; the primary stalks are quite stout, but short; the secondary branches are long and short, the tertiary branches are short and thick. Apices of the primary stalks are always smooth and completely devoid of the tertiary branches	4–6 pairs, secondary and tertiary braches are thick and about the same size	8 pairs, the pattern of branching is 'rosette'; the main stalk extends into at least four elongate papillae, each of which bears a number of shorter subdivisions	3–8 pairs, the primary stalks are tall and thick, secondary branches may be about the same size as the primary ones, tertiary branches are very short	5–7 pairs, the primary stalks are slender and rather narrow, giving rise to a number of graceful secondary branches, which decreases in size towards the ends of stalks, tertiary branches are short and thin	5–6 pairs, the primary stalks are robust and quite thick, secondary branches are rather short, the tertiary branches are quite short or absent	4–7 pairs, the primary stalks are very long and straight, secondary branches are quite thin, branched out almost perpendicular, tertiary branches are short, pointed and thin
Radula formula	33–41 × 8–14.1.8–14	32–38 × 6–8.1.6–8	28 × 6.1.6	37–48 × 9–14.1.9–14	29–49 × 7–14.1.7–14	41 × 8.1.8	34–61 × 11–20.1.11–20	15–21 × 5–8.1.5–8	16–20 × 7–9.1.7–9	28–43 × 6–14.1.6–14
Radula morphology	5–25 stout, sharply pointed denticles on border of median tooth cusp; 3–12 denticles on lateral teeth	Each sides of the cusp of the median tooth bear 11–14 small sharp denticles, sometimes denticles are missing; inner laterals with 4–6 denticles	The median tooth with 10 denticles on the each sides of the cusp, furrows are present, external lateral margins with 4–5 thin denticles	The median tooth is smooth, laterals are elongate and straight, slightly curved, bear 4–6 small denticles	The median tooth with 7–15 large, strong, and sharp denticles on the each sides of the cusp, the furrows are well pronounced and sharp. Laterals elongate, relatively wide, bear 2–7 long, strong, regularly placed denticles	The dorsal surface is prolonged into a bluntly triangular convex cusp. The lateral margins bear 16–19 denticles, similar in size along the margins. Laterals with 6–8 sharp denticles increasing in size towards the base of the tooth	Median tooth with sharp-pointed cusp, bearing 9–18 strongly developed, pointed denticles. Lateral teeth elongate, with a sharp cusp lacking denticles	The median tooth with an elongated triangular cusp, bearing 12–18 denticles on each side that continue down the dorsal side of the cusp as thin furrows; lateral teeth elongate, slightly curved toward the midline, with 4–5 sharp denticles on the outer border	The median tooth with triangular cusp, the denticles are reduced or missed, but sometimes the furrows remain visible; the outer border of the lateral teeth cusps carry 3–6 sharp and rather strong denticles	Rachidian tooth with 10–15 small denticles on each side of the cusp, the well-expressed furrows are long and thin. Laterals elongate with a long cusp, some laterals proximally with more delicate denticles, others have no denticles
Reproductive system	Prostate arranged in two concentric rings, crescent-shaped ampulla	Prostate arranged in a single concentric ring, ampulla is wide, short, and crescentic	Not described	Prostate arranged spherically around vas deferens, the ampulla is long, a little sinuous	Prostate arranged in a single concentric ring. The ampulla curled up like a doughnut	Not described, but protruding penis is unarmed	Prostate surrounds almost entire length of vas deferens. The ampulla is very long and tortuous	Prostate arranged spherically around vas deferens, ampulla is expanded and rounded	Prostate arranged spherically around vas deferens, ampulla elongate and sinuous	Prostate arranged spherically around vas deferens, ampulla strongly convoluted
References	Robilliard (1972), Pola & Stout (2008)	MacFarland (1966), Robilliard (1970), Pola & Stout (2008)	Valdes & Bouchet (1998)	Robilliard (1970), present study	Robilliard (1970), Pola & Stout (2008), Stout *et al.* (2010), present study	Baba (1949), Robilliard (1970), Pola & Stout (2008)	MacFarland (1966), Robilliard (1970)	Present study	Present study	Thollesson (1998), present study

Table 3. *Continued*

Species	***D. niveus* sp. nov.**	*D. noachi*	*D. orientalis*	*D. patricki*	*D. regius*	*D. robustus*	*D. rufus*	*D. subramosus*	*D. venustus*
Distribution	North-east Atlantic, the North, the Barents and the White seas	Bagabag Island, Papua New Guinea	North-west Pacific, Japan	Monterey Canyon and Santa Cruz Basin	Philippines, Indonesia, Malaysia	Arctic and North Atlantic	Alaska to Washington	British Columbia to Baja California	Alaska to Baja California
Body coloration	Milky white, pale pink with snow-white opaque pigment inside the end of rhinophoral sheath papillae, and dorsolateral processes	Translucent white with dark extensions of the digestive gland clearly visible	Milky white with chocolate-coloured spots and small yellow lines on the back	Reddish brown, with digestive gland visible through semi-translucent body as a purple mass, apices of dorsolateral processes, the papillae of the rhinophoral sheath, and velum are opaque white	White or yellow ground colour with dark purple/brown irregularly placed spots and purple/ brown bifurcations of the dorsolateral processes	Dark red with white spots or pale grey with small yellow spots	White or brick red body with red bifurcations on dorsolateral processes	White, brown, yellow, or orange, sometimes with white dorsolateral appendages and brown longitudinal lines running along dorsum	Variable: translucent, white, pale pink, brown, grey, yellow with brown stripes and spots, or any combination of these colour patterns
Branching of dorsolateral processes	5–10 pairs; all primary branches are strongly branched with secondary branches. The longest secondary branches bear short tertiary branches	4 pairs, the main central branch with two very small processes close to the tip; close to the base on the outer side there are two elongate papillae and slightly more distally on the inner side there are two more elongate papillae	4–6 pairs, with long primary stalk with secondary and very short tertiary branches	3 or 4 pairs, with robust primary stalks, with short conical secondary and very short tertiary branches	4–6 pairs, secondary and tertiary branches are thick and about the same size	6 or 7 pairs, relatively short and stout, not exceptionally arborescent, most of the branching being only short, thick offshoots	6–9 pairs, the primary stalks are thick, heavy, and very long, the secondary branches are also long, the tertiary branches are thin, terminating in a bushy tuft of fine filaments	3–6 pairs, with a 'rosette' pattern of branching; relatively few stout secondary branches. The tertiary branches are simple and short	4–6 pairs, secondary and tertiary branches are thick and about the same size
Radula formula	26–28 × 9–13.1.9–13	18 × 4.1.4	14–16 × 2.1.2	31 × 3–8.1.3–8	31–36 × 6–9.1.6–9	29–35 × 15–21.1.15–21	32–35 × 6–16.1.6–16	54–72 × 2–7.1.2–7	28–34 × 6–7.1.6–7
Radula morphology	Median tooth is smooth, but sometimes with visible thin furrows and reduced denticles; laterals with cusp slightly curved toward the midline and bear 4–8 denticles along its outer border	Median tooth is robust, the lateral margins of the thick strong cusp bear about 15 elongate denticles that decrease in size. Laterals with a thickened posterior margin that is elevated and prolonged into a strong pointed curve toward the midline, bearing 7–8 sharp denticles	Median tooth is large, with about 6–9 denticles on both sides of the cusp, inner lateral tooth bears 7 or 8 denticles on the outer margin, the outer tooth is smooth	Median tooth with strong central cusp and ~20 small denticles on each side, laterals elongate, with a sharp cusp lacking denticles	Median tooth is large with a strong triangular cusp directed upwards and backwards at an angle of about 45° to the base; the lateral margins are highly denticulate, bearing 15–20 long and pointed denticles that decrease in length as they approach the cusp; laterals with a series of 6 or 7 sharp denticles	Median tooth with strong central cusp and 15–20 small denticles on each side, laterals elongate, with a sharp cusp, the denticles are absent	The cusp of the median tooth is rounded or bluntly pointed at the apex and bears 6–28 small, blunt denticles diminishing in size towards the apex; lateral teeth with short, sharp denticles that do not project very far above the lateral border of the cusp	Median tooth with small cusp bearing 2–12 long heavy denticles; laterals are flat, often irregularly shaped. The sharp, long denticles are usually variable in shape and orientation	Median tooth large and strong, with 10–12 pointed denticles; lateral teeth thin, elongate, flattened plates, the posterior margin prolonged into a strong point bearing denticles
Reproductive system	Prostate arranged spherically around vas deferens; ampulla is large, with expansion in the midline	Not described	Not described	Prostate arranged spherically around vas deferens, ampulla sinuous and short	Prostate arranged as a flattened sphere ring around vas deferens, ampulla is sausage-shaped	Prostate arranged in a single concentric ring, ampulla is long and narrow	Prostate is very large and arranged spherically around vas deferens, ampulla is long and narrow	Prostate arranged in a single concentric ring, ampulla is short, thick, and crescentric	Prostate arranged spherically around vas deferens
References	Present study	Pola & Stout (2008)	Baba (1932)	Stout *et al.* (2011)	Pola & Stout (2008)	Robilliard (1970, 1971)	Robilliard (1970)	MacFarland (1966), Robilliard (1970)	MacFarland (1966), Stout *et al.* (2010)

D. frondosus (Roginskaya, 1962) and *D. dalli* (Roginskaya, 1987). Indeed, radula features are similar to *D. dalli*. Median tooth in adult specimens of *D. niveus* sp. nov. is smooth, as in *D. dalli*; however, *D. niveus* sp. nov. and *D. dalli* are well distinguished by the morphology of dorsolateral processes, pattern of the coloration, and details of the radula. Long and short secondary branches in *D. niveus* sp. nov. branched off throughout all primary stalk and long secondary branches, which carry numerous small tertiary branches (Fig. 8F). *Dendronotus dalli* also has long and short secondary branches, but apices of the primary stalks are always smooth and completely devoid of the secondary and tertiary branches (Fig. 8G). In addition, apices of primary stalks covered with opaque white pigment, always on the surface of the processes and never inside. Large adult specimens of *D. dalli* from the north-west Pacific (Kamchatka), close to the type locality of this species in the Bering Strait, invariably possess white pigment on the surface of the processes (Fig. 11). In *D. niveus* sp. nov. the white pigment is instead found inside the processes and shines through the semitransparent body wall (Fig. 14A–C). This feature is well defined only in the juveniles, and is often absent in the large adults from distant localities and different depths (Barents and White seas) (Fig. 14D, E). The radulae of the juvenile and the smaller specimens of *D. niveus* sp. nov. and *D. dalli* are possible to differentiate (Figs 12, 15). The median tooth of *D. niveus* sp. nov. bears numerous (14–16 on each side) small flattened denticles that continue down the dorsal side of the tooth, and form thin shallow furrows. Even in large specimens the denticles become reduced, but the furrows remain visible. The cusp of *D. dalli* juvenile median tooth possesses only some irregular denticles, but the furrows are absent. From the other species that have the same colour pattern (white specimens of *D. frondosus*, *D. venustus*, *D. lacteus*, and *D. albus*), *D. niveus* sp. nov. clearly differs in the radular morphology: median tooth of these four species is always strongly denticulated and never smooth, as in *D. niveus* sp. nov. Lateral teeth are also different. *Dendronotus lacteus* has more robust and short laterals without denticles. In *D. venustus* and *D. frondosus* the cusp of the lateral tooth bears many well-defined denticles, without any sign of furrows. In addition, all these species can be distinguished from *D. niveus* sp. nov. by the pattern of the branching of the dorsolateral processes (Fig. 8). In this study another species that also possesses a smooth median tooth is described: *D. kamchaticus* sp. nov. (Figs 16A, B, 17). This new species clearly differs from *D. niveus* sp. nov. in lateral teeth features (lateral teeth cusps bear a number of well-defined denticles, the furrows are small or absent, teeth are shorter), colour (*D. kamchaticus* sp. nov. is always variegated, we have not found uniform white or pinkish specimens), pattern of the branching of the dorsolateral processes (Fig 8D, F), and features of the reproductive system (Figs 13B, 18A). Little known *D. elegans* from the west Atlantic (Verrill, 1880; Bleakney, 1996) apparently also possesses smooth central teeth and needs further study. Molecular data based on the genes *COI*, *16S*, *H3*, and *28S* clearly place *D. niveus* sp. nov. in a separate clade, distant from both *D. dalli* and *D. frondosus* (Fig. 24). The morphological differences between *D. niveus* sp. nov. and the other species of *Dendronotus* are summarized in Table 3.

DENDRONOTUS KAMCHATICUS SP. NOV.

FIGURES 6E, 8D, 16A, B, 17, 18A

Type material

Holotype: ZMMU Op-245, *L* = 12 mm, dissected, north-west Pacific, Kamchatka, Avachinskiy Bay, Cape Baraniy, rocky bottom, 7 m depth, 15.vi.2010, coll. D.B. Semenov.

Paratypes: ZMMU Op-246, four spcs, *L* = 6, 8, 9, and 10 mm, three dissected, north-west Pacific, Kamchatka, Avachinskiy Bay, 7 m depth, 6.viii.2008, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-247, three spcs, *L* = 2–5 mm, dissected, north-west Pacific, Kamchatka, Avachinskiy Bay, 1.viii.2008, coll. T.A. Korshunova, A.V. Martynov.

Etymology

After Kamchatka Peninsula in north-east Russia.

External morphology (Figs 8D, 16A, B)

Body elongated, laterally compressed. Foot narrow, tail short. Oral veil with between four and six lip papillae and branched appendages. Primary stalks of veil appendages tall and slender, giving rise to numerous short secondary branches. Rhinophoral sheath divided into five or six crown papillae that are about the same length. The short lateral papillae (max one-third of the sheath length) branches off the sheath base and is expanded with small secondary branches. The rhinophores bear between five and 25 lamellae. Five or six pairs of dorsal appendages. Primary stalks of cerata short and bulbous. Secondary branches of dorsal appendages short; tertiary branches of dorsal appendages short or absent (Fig. 8D). Digestive gland diverticula penetrate cerata and rhinophoral branched processes. These diverticula in first part of cerata and rhinophores originate from anterior lobe of digestive gland; others arise from posterior lobe. Anal opening on right side of body about midway between first and second pair of dorsal appendages. Reproductive openings lateral near the first pair of cerata on right side.

Colour (Fig. 16A, B)

Background colour is transparent white, with complex pattern of light, dark, and red–brown spots and stripes.

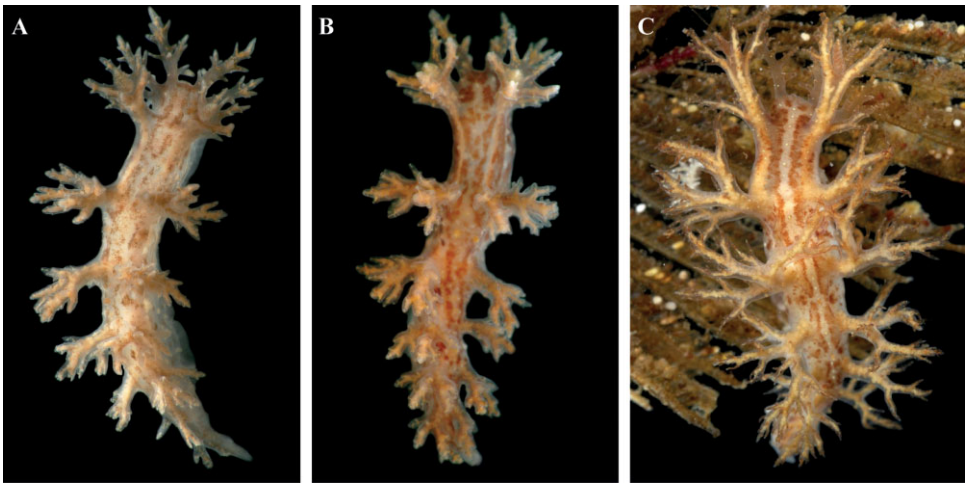

Figure 16. Living animals of *Dendronotus* spp. A, ***Dendronotus kamchaticus* sp. nov.,** north-west Pacific, Kamchatka, Avachinskiy Bay, 10 mm in length, photo by T.A. Korshunova, paratype ZMMU Op-246; B, ***Dendronotus kamchaticus* sp. nov.,** north-west Pacific, Kamchatka, Avachinskiy Bay, 8 mm in length, photo by T.A. Korshunova, paratype ZMMU Op-246; C, ***Dendronotus kalikal* sp. nov.,** north-west Pacific, Kamchatka, Avachinskiy Bay, 10 mm in length, photo by N.P. Sanamyan, holotype ZMMU Op-283.

On dorsal side spots and stripes merge and form characteristic striped pattern. Lateral sides of body devoid of stripes but covered with brown spots. Brown branches of digestive gland clearly visible through thin walls of rhinophoral sheathes, dorsal appendages, and velar papillae. Lamellae of rhinophores light brown. All body, including rhinophoral sheathes, cerata, and upper parts of foot covered with white and golden pigment spots that are often placed inside special low tubercles.

Jaws (Fig. 6E)

Dorsal process of jaws strong; length about one-quarter of jaw body length. Inclined posteriorly at about 15°. Length of dorsal processes of jaws about one-third length of jaw body, strong at base, but becoming transparent and subulate posteriorly. Denticles absent on masticatory border.

Radula (Fig. 17)

Radula formula: 18 × 8–9.1.8–9 (holotype ZMMU Op-245); 16 × 8.1.8 (paratype ZMMU Op-247); 20 × 7–8.1.7–8 (paratype ZMMU Op-246). Median tooth large and strong, with quadrangular base and triangular cusp. Median tooth of subadult specimens bear between ten and 12 small, relatively sharp denticles that continue down dorsal side of cusp as thin furrows (Fig. 17E). In adult specimens denticles absent, tooth completely smooth, sometimes with faint furrows (Fig. 17A, C, D). Median tooth of juvenile specimens highly denticulated, with well-expressed conical cusp and between three and six denticles on each side (Fig. 17G, H). Colour of oldest median teeth is light yellow, others transparent. Between seven and nine lateral teeth, each consisting of elongate, flattened plate and cusp. Outer border of cusps bearing between three and six sharp and strong denticles (Fig. 17B–H). Innermost lateral tooth thin, delicate, and highly denticulated, one or two outermost teeth narrow and plate-like, with straight apex (in juvenile specimens) or thin and flattened (in adults), and do not bear denticles.

Reproductive system (Fig. 18A)

Triaulic. Large white ovotestis composed of many rounded lobules, and leading to hermaphrodite duct that expands into elongate sinuous ampulla. Prostata consisting of seven or eight oval alveoli, distal part of vas deferens narrow and winding, expanding to narrow elongate penis. Oviduct connects through insemination duct into female gland complex. Vagina long, strait, with small bursa copulatrix, gradually narrows into rounded seminal receptaculum. Long insemination duct emerges from seminal receptaculum and connects into oviduct and female gland mass. Female genital aperture opens posterior to penis on right side of body, between first and second pairs of dorsolateral processes.

Ecology

Found subtidally at 7–10 m in depth. Inhabits brown algae or rocks covered with hydrozoan colonies (Thecaphora). Egg masses are unknown.

Distribution

North-west Pacific, Kamchatka, Avachinskiy Bay; probably has wider distribution.

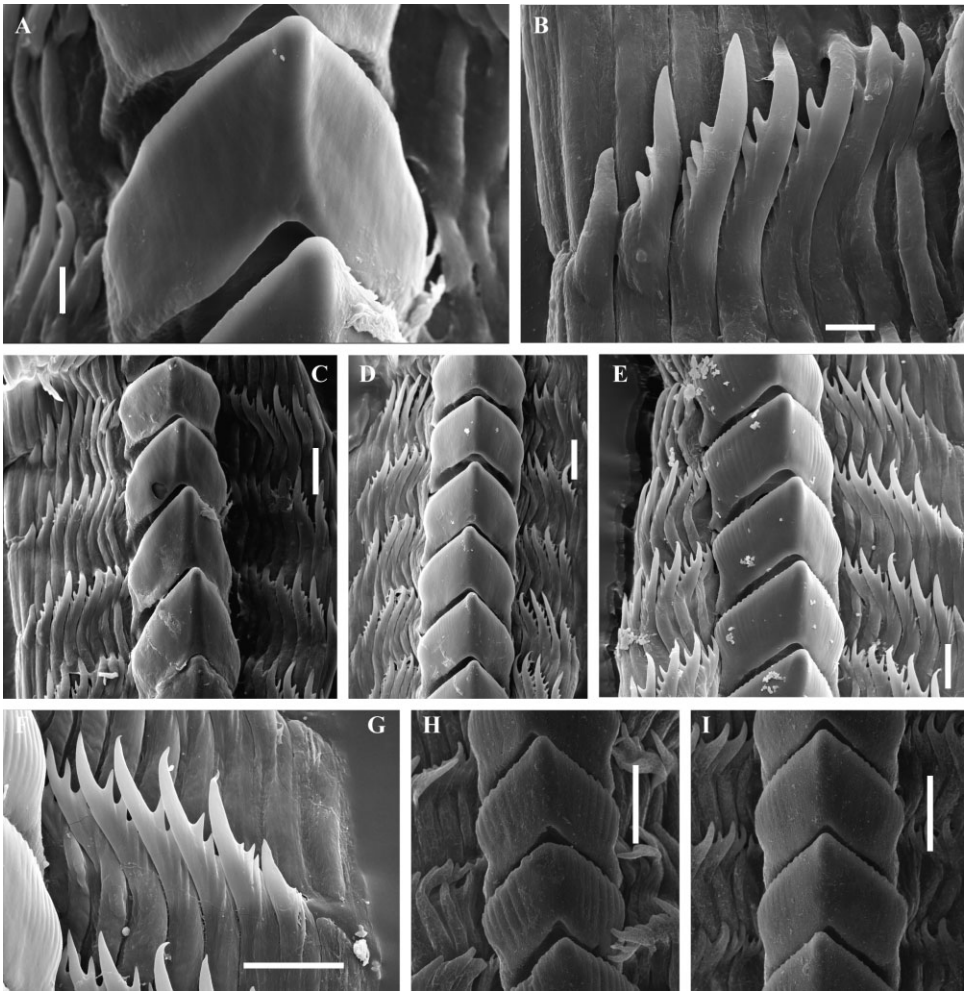

Figure 17. ***Dendronotus kamchaticus*** **sp. nov.** Scanning electron micrographs of the radula. A, holotype ZMMU Op-245, specimen 12 mm in length, rachidian tooth, scale bar = 30 μm. B, holotype ZMMU Op-245, lateral teeth, scale bar = 10 μm. C, holotype ZMMU Op-245, rachidian and lateral teeth, scale bar = 30 μm. D, paratype ZMMU Op-246, specimen 10 mm in length, rachidian and lateral teeth, scale bar = 30 μm. E, paratype ZMMU Op-246, specimen 9 mm in length, rachidian and lateral teeth, scale bar = 30 μm. F, paratype ZMMU Op-246, specimen 9 mm in length, lateral teeth, scale bar = 30 μm. G, paratype ZMMU Op-249, specimen 5 mm in length, rachidian and lateral teeth, scale bar = 30 μm. H, paratype ZMMU Op-249, specimen 3 mm in length, rachidian teeth, scale bar = 10 μm.

Remarks

Dendronotus kamchaticus sp. nov. is clearly separated from other species of the genus *Dendronotus* according to both morphological and molecular data (Table 3; Fig. 24). *Dendronotus kamchaticus* sp. nov. shares similar external morphology (including pattern of branching of the dorsal appendages and spotted coloration) to *D. frondosus* and *D. venustus*, but differs considerably from both species in radular morphology. The median tooth of both *D. frondosus* and *D. venustus* invariably shows the presence of numerous sharpened denticles, with large furrows on the outer surface of the tooth (Figs 4, 5). Adult specimens of *D. kamchaticus* sp. nov. instead have a completely smooth median tooth (Fig. 17A, C). Remarkably, juvenile and subadult specimens of *D. kamchaticus* sp. nov. possess between ten and 12 small denticles on each side of the median tooth that expand to the furrows (Fig. 17E, G, H), but the furrows are shorter and thinner than in *D. frondosus* and *D. venustus*. The details of body coloration also differ: all specimens studied of *D. kamchaticus* sp. nov. possess a regular striped pattern on the dorsum (Fig. 16A, B), whereas *D. venustus* and *D. frondosus* usually have a more irregular pattern of dorsal blotches, which sometimes are completely absent (Figs 1–3). In addition, these three species discussed have differing morphology of the reproductive system. The ampulla of *D. kamchaticus* sp. nov. is elongate and

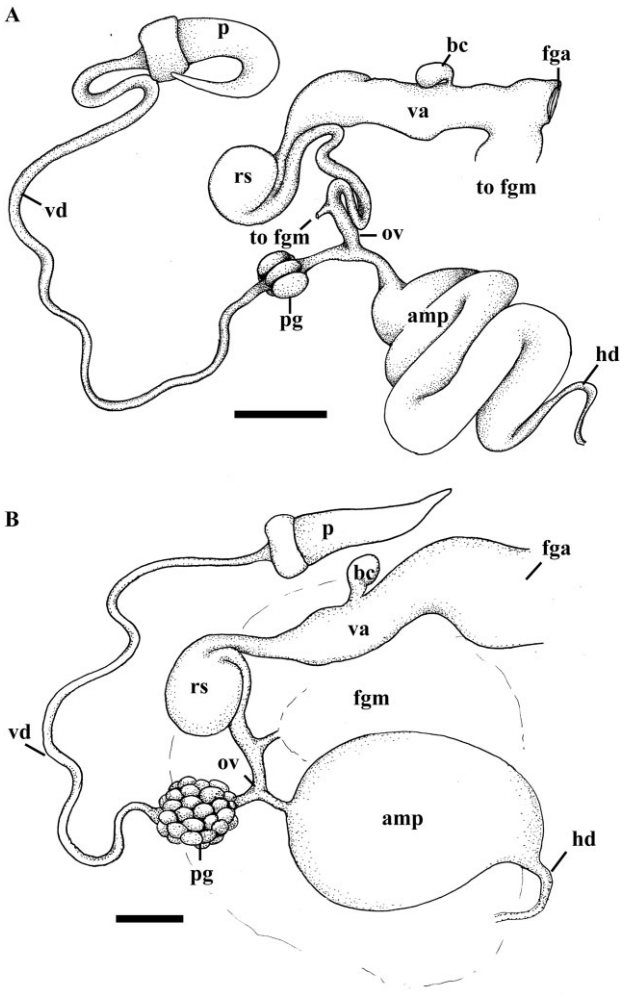

Figure 18. Reproductive system. A, ***Dendronotus kamchaticus* sp. nov.,** ZMMU Op-245. B, ***Dendronotus kalikal* sp. nov.,** ZMMU Op-285. Abbreviations: amp, ampulla; bc, bursa copulatrix; fga, female genital aperture; fgm, female gland mass; hd, hermaphroditic duct; ov, oviduct; p, penis; pg, prostate; rs, receptaculum seminis; va, vagina; vd, vas deferens. Scale bar: 1 mm.

sinuous, whereas *D. frondosus* has a wide a semicircular ampulla. *Dendronotus venustus* is characterized by the crescent-shaped ampulla. *Dendronotus dalli* shares with *D. kamchaticus* sp. nov. the completely smooth adult median tooth, but other characters are very different. The colour of *D. dalli* is milky white or rose, with white pigment scattered over appendages (Fig. 11). The masticatory border of *D. dalli* bears low denticles that are absent in *D. kamchaticus* sp. nov. The lateral radular teeth of *D. dalli* with very long, narrow plates of lateral teeth, and cusps that are slightly inclined towards the midline, and away from the long axis of the base of the tooth (Fig. 12D, F). The sharp, irregularly arranged and not very long denticles are situated along the proximal, lateral borders, whereas specimens of *D. kamchaticus* sp. nov. possess curved laterals with strong sharp denticles on their outer borders. Regarding the reproductive system, the prostate of *D. dalli* consist of more alveoli (30–40) than in *D. kamchaticus* sp. nov. (seven or eight) (Figs 13A, 18A). Another new species from the Kamchatka waters, *D. kalikal* sp. nov., is clearly distinguished from *D. kamchaticus* sp. nov. by a number of both external and internal characters. *Dendronotus kalikal* sp. nov. possesses more elongate and narrow primary stalks of dorsal appendages, secondary branches are rather long, and tertiary branches are short and pointed, whereas the primary stalks of *D. kamchaticus* sp. nov. are fingerlike and swollen, secondary branches are short, and tertiary branches are absent (Fig. 8D, E). Adult specimens of *D. kalikal* sp. nov. have a median tooth that possesses a number of well-defined denticles with thin furrows (Fig. 19), whereas in *D. kamchaticus* sp. nov. the denticles and furrows are absent or strongly reduced. Molecular data based on the genes *COI*, *16S*, *H3*, and *28S* clearly place *D. kamchaticus* sp. nov. in a separate clade, distant from the other species of the genus *Dendronotus* (Fig. 24). The morphological differences between *D. kamchaticus* sp. nov. and the other *Dendronotus* species are summarized in Table 3.

DENDRONOTUS KALIKAL SP. NOV.

FIGURES 6F, 8E, 16C, 18B, 19

Type materials

Holotype: ZMMU Op-283, *L* = 9 mm, dissected, north-west Pacific, Kamchatka, Avachinsky Bay, Starichkov Island, 14–16 m depth, 23.viii.2009, coll. N.P. Sanamyan.

Paratypes: ZMMU Op-284, four spcs, *L* = 2–7 mm, three dissected, north-west Pacific, Kamchatka, Avachinsky Bay, Starichkov Island, 14–16 m depth, 15.viii.2009, coll. N.P. Sanamyan. ZMMU Op-285, one spc., *L* = 10 mm, dissected, Bering Strait, 60 m depth, v.2006, coll. B.I. Sirenko. ZMMU Op-349, eleven spcs, *L* = 3–8 mm, three dissected, 20–22 m depth, 15.ix.2012, coll. N.P. Sanamyan.

Etymology

After 'kalikal' (Koryak, one of the indigenous languages of Kamchatka), meaning variegated pattern.

External morphology (Figs 8E, 14C)

Body elongate, laterally compressed. Foot narrow, tail short. Oral veil with between four and six lip papllae and four or five veil processes. Rhinophoral sheath with five branched appendages. Small lateral papillae (max one-third of sheath length) branches off sheath base and bears small secondary branches. Rhinophores bear between six and ten lamellae, with between five and

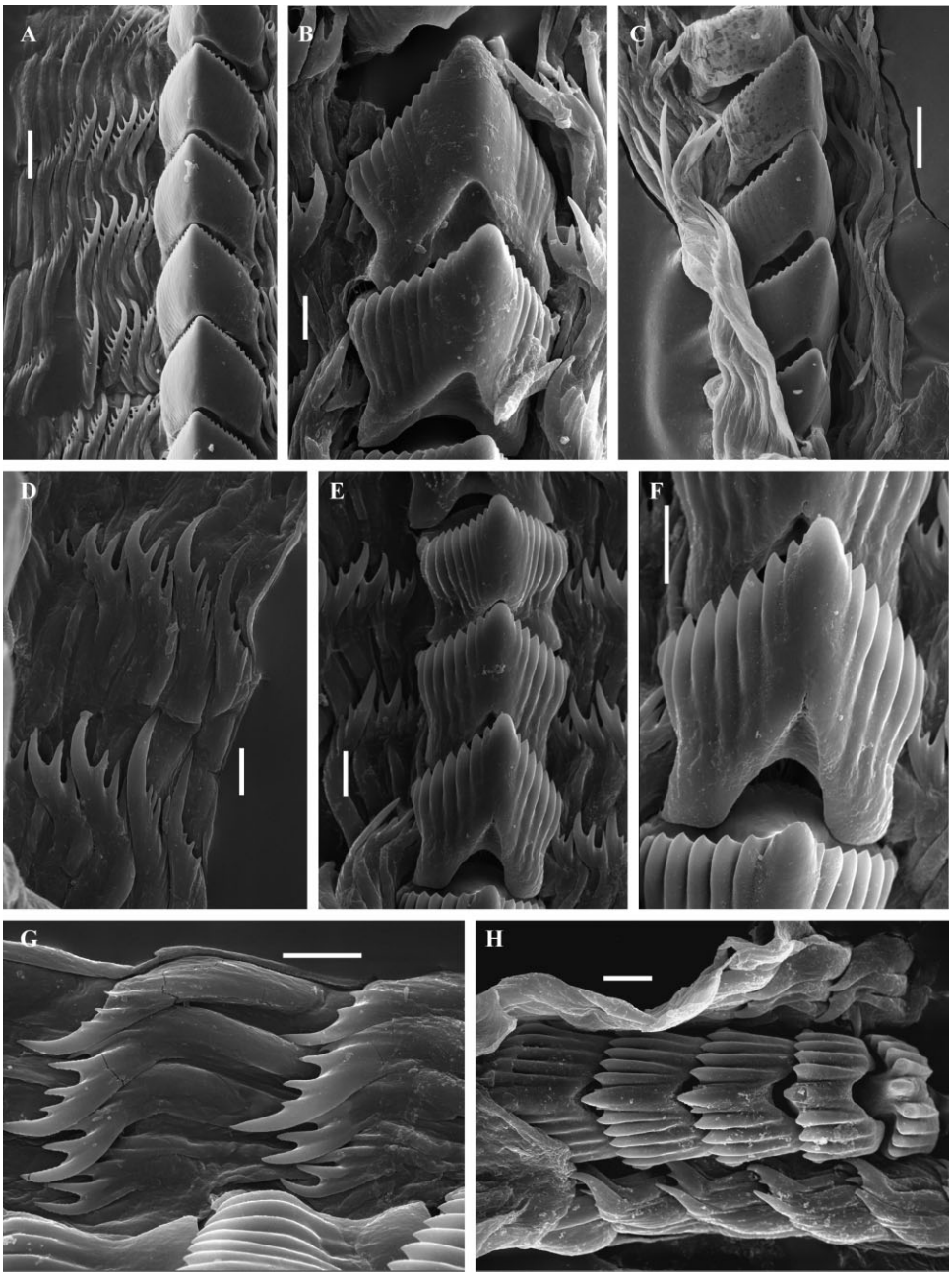

Figure 19. ***Dendronotus kalikal*** **sp. nov.** Scanning electron micrographs of the radula. A, paratype ZMMU Op-285, specimen 18 mm in length, rachidian and lateral teeth, scale bar = 30 μm. B, holotype ZMMU Op-283, specimen 10 mm in length, rachidian teeth, scale bar = 10 μm. C, holotype ZMMU Op-283, specimen 10 mm in length, rachidian and lateral teeth, scale bar = 30 μm. D, holotype ZMMU Op-283, specimen 10 mm in length, lateral teeth, scale bar = 10 μm. E, paratype ZMMU Op-284, specimen 6 mm in length, rachidian and lateral teeth, scale bar = 10 μm. F, paratype ZMMU Op-284, specimen 6 mm in length, rachidian tooth, scale bar = 10 μm. G, paratype ZMMU Op-284 specimen, 6 mm in length, lateral teeth, scale bar = 10 μm. H, paratype ZMMU Op-284, specimen 2 mm in length, rachidian and lateral teeth, scale bar = 10 μm.

seven pairs of dorsal appendages. Primary stalks slender and narrow, with numerous thin secondary branches. Tertiary branches short and pointed (Fig. 8E). Digestive gland diverticula present in pairs of cerata and in rhinophoral appendages. Anal opening on right side of body about midway between first and second pair of dorsal appendages. Reproductive openings lateral, near first pair of cerata on right side.

Colour (Fig. 14C)
Background colour is transparent white with complex pattern of light, dark, and red–brown spots and stripes. On dorsal side spots and stripes fused and form characteristic striped pattern. Laterally, body covered by brown spots, stripes are absent. Brown branches of digestive gland clearly visible through fine body wall in rhinophoral sheath and dorsal appendages, but absent in velar processes. Lamellae of rhinophores are light brown. Low tubercles, with white or golden pigment inside, cover all body except foot.

Jaws (Fig. 6F)
Length of dorsal process about one-third of jaw body length. Inclined posteriorly at about 30°. Masticatory process dark at base, transparent and thin posteriorly, bearing a single row of rodlets.

Radula (Fig. 19)
Radula formula: 21 × 6–8.1.6–8 (holotype ZMMU Op-283); 15 × 5–6.1.5–6 (paratype ZMMU Op-284); 24 × 7–8.1.7–8 (paratype D-285). Median tooth strong and elongated, triangular, bearing 12–18 denticles on each side of the cusp and thin furrows (Fig. 19A). Older median teeth light yellow, others transparent. Lateral teeth elongate, slightly curved towards the midline (Figure 19A, D, G). Outer border of cusp with four or five sharp denticles. Innermost lateral tooth thin, delicate, and highly denticulated, one or two outermost teeth narrow, plate-like, with straight apex and reduced cusp. In juvenile specimens rachidian tooth possesses well-differentiated conical cusp with four or five strong denticles on both sides and large deep furrows (Fig. 19E, F, H). In subadult specimens the tooth shape changes from rectangular to triangular, cusp reduces, and number of denticles increases (Fig. 19B, C). Number of lateral teeth also increases from two in juveniles (Fig 19H) to eight in adult specimens (Fig. 19A).

Reproductive system (Fig. 18B)
Triaulic. Large light-yellow ovotestis composed from numerous rounded lobules, leading to hermaphrodite duct. It expands into a small rounded ampulla. Prostata consists of ~20 small oval alveoli, distal part of vas deferens narrow and winding, expands to elongated penis. Oviduct connects through insemination duct into female gland complex. Vagina long, sinuous, extended distally, with small bursa copulatrix, gradually narrowing into rounded seminal receptaculum. Insemination duct emerges from seminal receptaculum and connects into oviduct and female gland mass. Female genital aperture opens posterior to penis on right side of body, between first and second pairs of dorsolateral processes.

Ecology
Found subtidally at 14–60 m in depth. Inhabits brown algae or rocks covered with hydrozoan colonies (Thecaphora). Features of reproduction are unclear.

Distribution
North-west Pacific: Kamchatka, Avachinskiy Bay, and Bering Strait. Egg masses are unknown.

Remarks
Dendronotus kalikal sp. nov. is well separated from other species of *Dendronotus* according to both morphological and molecular data (Fig. 24; Table 3). *Dendronotus kalikal* sp. nov. shows similarity to *D. frondosus* and *D. venustus*. The general body coloration in each species is characterized by the presence of brown and yellow spots, and also low tubercles with golden and white pigment; however, whereas in *D. frondosus* and *D. venustus* their arrangement is rather irregular (Figs 1–3), in *D. kalikal* sp. nov. they form a regular striped pattern. The branching of dorsolateral processes is also different: secondary and tertiary branches in *D. frondosus* and *D. venustus* are thick (Fig. 8A), whereas tertiary branches in *D. kalikal* sp. nov. are thin, almost subulate, and processes appear to be more elegant (Fig. 8E). Rachidian teeth are rather similar in these three species, but denticles are further reduced in *D. kalikal* sp. nov., their number is fewer, and the tooth looks more elongate. In *D. frondosus* and *D. venustus* the furrows are more pronounced and sharp (Figs 4, 5). In radula features, this new species resembles *D. albus*, because of the presence of furrows, and the number and arrangement of denticles; however, there are several of considerable differences. The furrows on median teeth in *D. albus* are reduced to completely absent in some specimens (Pola & Stout, 2008). Also, lateral teeth in *D. kalikal* sp. nov. are much more elongate and narrow. In addition, there are a number of reliable differences in the external features (coloration, shape of the body, and branching patterns of the dorsolateral processes). *Dendronotus kalikal* sp. nov. clearly differs from the other species that inhabits the shallow waters of Kamchatka, *D. dalli*, in radula morphology: median teeth of *D. dalli* are smooth, and borders of lateral teeth are longer and straighter with not very well-defined cusps (Fig. 12). We have already discussed the comparison of *D. kalikal* sp. nov. with another new species, *D. kamchaticus* sp. nov., from the waters of Kamchatka above. Molecular data based on the genes *COI*, *16S*, *H3*, and *28S* clearly place *D. kalikal* sp. nov. in a separate clade distant from the other species of the genus *Dendronotus* (Fig. 24). The morphological differences between *D. kalikal* sp. nov. and the other *Dendronotus* species are summarized in Table 3.

Dendronotus robustus Verrill, 1870

Figures 6G, 8C, 20–23

Dendronotus robustus Verrill, 1870: 405–406, fig. 1; Robilliard, 1970: 450–451; Filatova & Zatsepin, 1948; Roginskaya, 1980: 80–84, fig. 1; 1987: 172–173; Martynov & Korshunova, 2011: 157–158.

?*Dendronotus velifer* Sars, 1878: 238–239, pl. 28, fig. 2, pl. 15, fig. 4.

Non *Dendronotus velifera sensu* Pruvot-Fol, 1954 (= *D. lacteus*).

Non *Dendronotus velifer sensu* Nordsieck, 1972 (= *D. lacteus*).

Type material

Lost (Johnson, 1989).

Material examined

ZMMU Op-296, three spcs, *L* = 30–45 mm, one dissected, Barents Sea, R/V 'Romuald Muklevich', sta. 61, 69°00.380′N, 40°02.650′E, 135–137 m depth, 22.viii.2003, coll. P.A. Lyubin. ZMMU Op-341, one spc., Barents Sea, R/V 'Romuald Muklevich', sta. 53, 72°01.082′N, 37°58.636′E, depth 287–290 m depth, 20.viii.2003, coll. P.A. Lyubin. ZMMU Op-342, two spcs, one dissected, Barents Sea, R/V 'Romuald Muklevich', sta. 48, 69°32.371′N, 38°32.880′E, 100–110 m, 19.viii.2003, coll. P.A. Lyubin. ZNNU Op-343, two spcs, *L* = 13 and 30 mm, dissected, Barents Sea, Dalne-Zelenetskaya Bay, 5–10 m depth, 15.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU Op-344, two spcs, *L* = 10 and 30 mm, dissected, Barents Sea, Dalne-Zelenetskaya Bay, 5–10 m depth, 15.viii.2012, coll. T.A. Korshunova, A.V. Martynov. ZMMU

Figure 20. *Dendronotus robustus* Verrill, 1870. Living animals. A, Barents Sea, Dalne-Zeleneckaya Bay, 30 mm in length, photo by T.A. Korshunova, ZMMU Op-343. B, Barents Sea, Varangerfjord, 15 mm in length, photo by T.I. Antokhina; C, Barents Sea, R/V 'Dalnie Zelentsy', st. MB-5, 69°07.8′N, 58°05.5′E, 12 mm in length, photo by O.L. Zimina. D, Barents Sea, Dalne-Zeleneckaya Bay, 25 mm in length, photo by T.A. Korshunova, ZMMU Op-344. E, Barents Sea, Dalne-Zeleneckaya Bay, 12 mm in length, photo by T.A. Korshunova, ZMMU Op-343. F, Barents Sea, Dalne-Zeleneckaya Bay, 12 mm in length, photo by T.A. Korshunova, ZMMU Op-343.

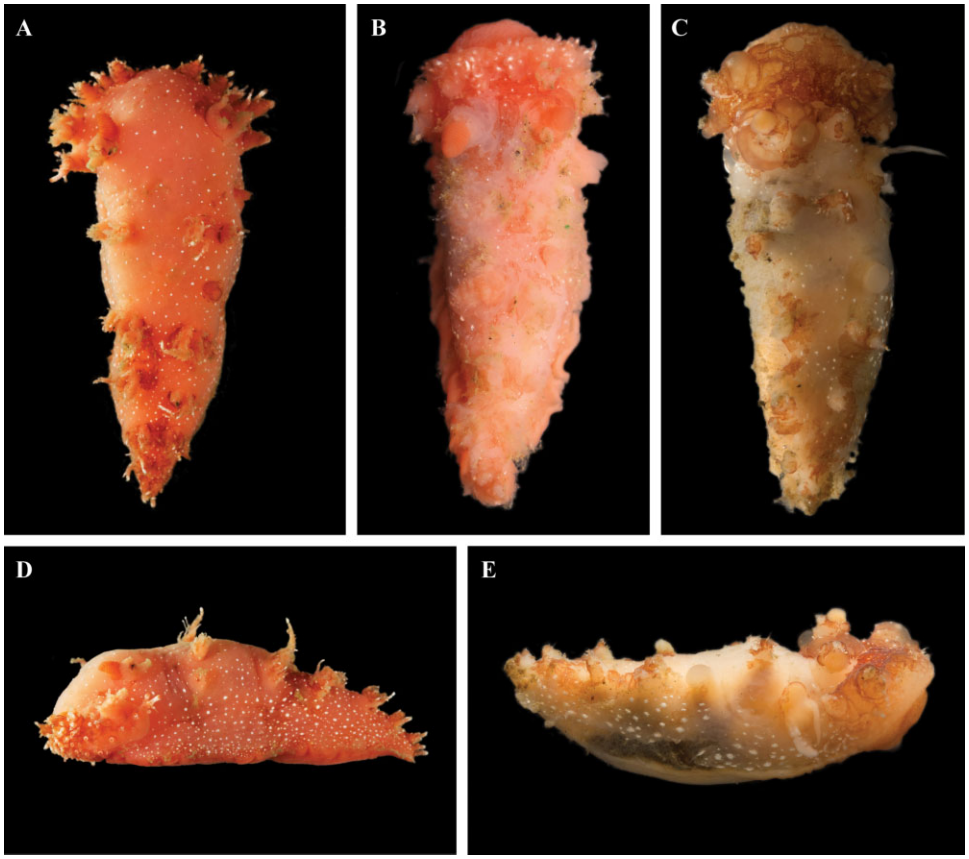

Figure 21. *Dendronotus robustus* Verrill, 1870. Living animals. A, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 25 mm in length, ventral view, photo by A.A. Semenov. B, Kara Sea, R/V 'Dalnie Zelentsy'. sta. 2vp-37, 73°48.6′N, 75°35.1′E, 23 mm in length, photo by O.L. Zimina, ZMMU Op-348; C, Barents Sea, 'R/V Dalnie Zelentsi', sta. CB-23, 75°01.6′N, 38°00.9′E, 33 mm in length, dorsal view, photo by O.L. Zimina, ZMMU Op-395. D, White Sea, Kandalaksha Bay, Velikaya Salma Strait, 25 mm in length, lateral view, photo by A.A. Semenov. E, Barents Sea, 'R/V Dalnie Zelentsi', sta. CB-23, 75°01.6′N, 38°00.9′E, 33 mm in length, lateral view, photo by O.L. Zimina, ZMMU Op-395.

Op-345, one spc., dissected, White Sea, 20 m depth, vii.2001, coll. unknown. ZMMU Op-346, three spcs, L = 23–35 mm, dissected, Bering strait, R/V 'Healy', sta. 96, 63°973.766′N; 173°061.99′E, 67 m depth, 30.v.2006, coll. B.I. Sirenko. ZMMU Op-347, two spcs, L = 25 and 30 mm, one dissected, Bering strait, R/V 'Healy', sta. 41 63°035.11′N; 173°455.58′E, 64 m depth, 20.v.2006, coll. B.I. Sirenko. ZMMU Op-360, one spc., dissected, Bering strait, R/V 'Healy', sta. 26, 63°106.302′N, 173°088.25′E, 72 m depth, 16.v.2006, coll. B.I. Sirenko. ZMMU Op-348, one spc., L = 28 mm, dissected, Kara Sea, R/V 'Dalnie Zelentsy', sta. 2vp-37, 73°48.6′N, 75°35.1′E, 21 m depth, 13.ix.2012, coll. O.L. Zimina. ZMMU Op-390, eight spcs, four dissected, Barents Sea, R/V 'Dalnie Zelentsy', st. MB-2, 68°56.9′N, 57°56.9′E, 13 m depth, 22.vii.2013, coll. O.L. Zimina. ZMMU Op-391, three spcs, one dissected, Barents Sea, R/V 'Dalnie Zelentsy', st. MB-5, 69°07.8′N, 58°05.5′E, 18 m depth, 19.vii.2013, coll. O.L. Zimina. ZMMU Op-392, six spcs, three dissected, Barents Sea, R/V 'Dalnie Zelentsy', st. MB-13, 69°14.8′N, 57°59.6′E, 19 m depth, 19.vii.2013, coll. O.L. Zimina. ZMMU Op-393, one scps, dissected, Barents Sea, R/V 'Dalnie Zelentsy', st. MB-14, 69°08.3′N, 57°48.0′E, 17 m depth, 18.vii.2013, coll. O.L. Zimina. ZMMU Op-395, one spc., dissected, Barents Sea, R/V 'Dalnie Zelentsy', st. CB-23, 75°01.6′N, 38°00.9′E, 182–184 m depth, 11.vi.2013, coll. O.L. Zimina. ZMMU Op-396, one spc., dissected, Barents Sea, R/V 'Dalnie Zelentsy', st. CB-17, 75°14.4′N, 39°45.4′E, 234–237 m depth, 11.vi.2013, coll. O.L. Zimina.

External morphology (Figs 8C, 20, 21)

Body and foot broad. Oral veil large with numerous lip papillae and between ten and 12 massive branched processes. Rhinophores with 16–20 lamellae. Rhinophore sheath possesses between four and six small secondary branched appendages. Lateral papilla absent.

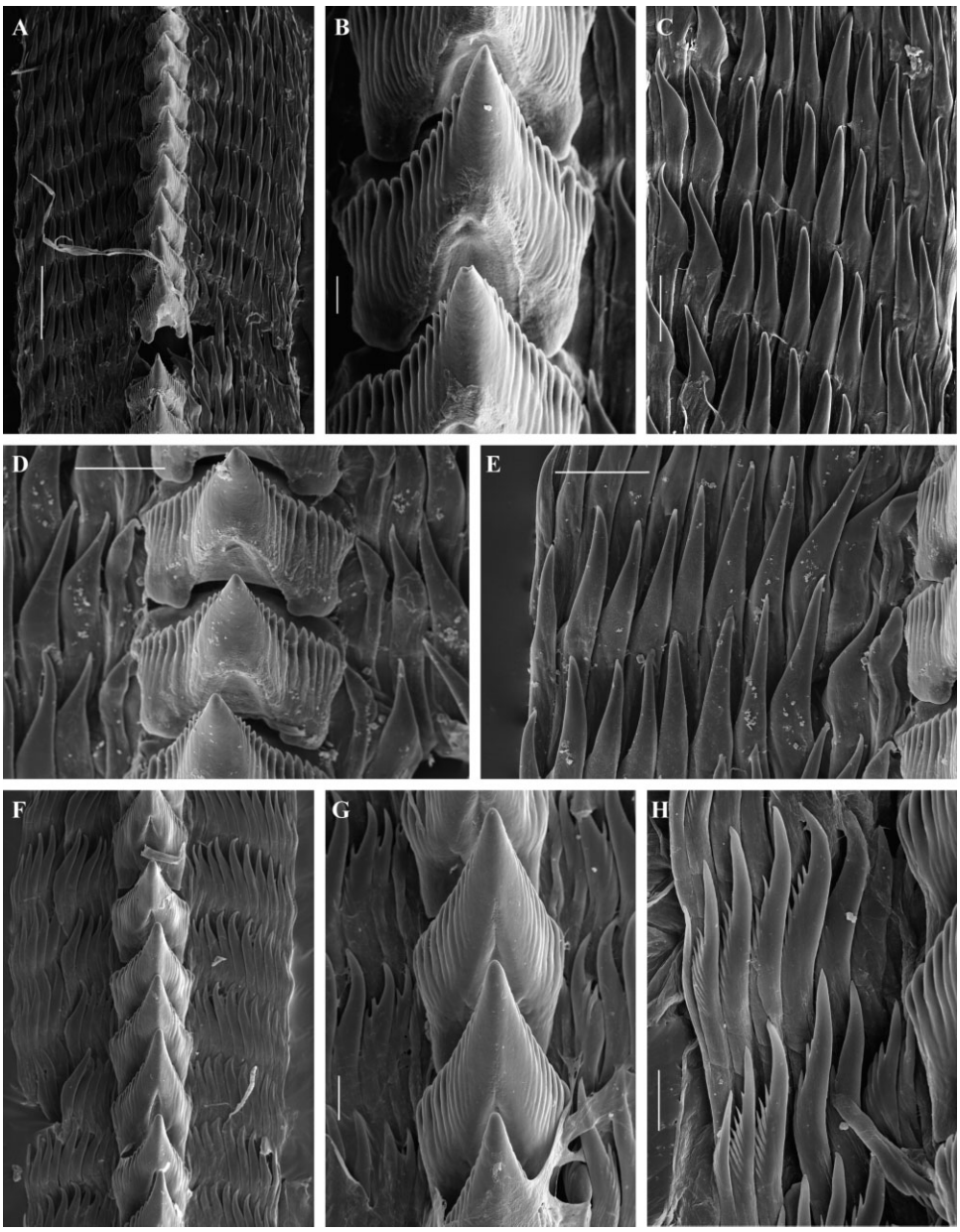

Figure 22. *Dendronotus robustus* Verrill, 1870. Scanning electron micrographs of the radula. A, ZMMU Op-347, specimen 20 mm in length, rachidian and lateral teeth, scale bar = 300 μm. B, ZMMU Op-347, specimen 20 mm in length, rachidian tooth, scale bar = 30 μm. C, ZMMU Op-347, specimen 20 mm in length, lateral teeth, scale bar = 100 μm. D, ZMMU Op-346, specimen 30 mm in length, rachidian teeth, scale bar = 100 μm. E, ZMMU Op-346, specimen 30 mm in length, lateral teeth, scale bar = 100 μm. F, ZMMU Op-390, specimen 15 mm in length, rachidian and lateral teeth, scale bar = 100 μm. G, ZMMU Op-344, specimen 10 mm in length, rachidian teeth, scale bar = 10 μm. H, ZMMU Op-344, specimen 10 mm in length, lateral teeth, scale bar = 10 μm.

Relatively short and stout dorsolateral processes are arranged in between four and seven pairs, their size and degree of branching decreasing towards the tail. Dorsolateral processes branched with mediate secondary branches, tertiary branches are short if present (Fig. 8C). Digestive gland diverticula penetrate to dorsolateral processes and to rhinophoral branched processes. Anal opening is on right side of body along dorsolateral line, about midway between first and second pair of dorsolateral processes. Reproductive openings placed laterally near first pair of dorsolateral processes on right side.

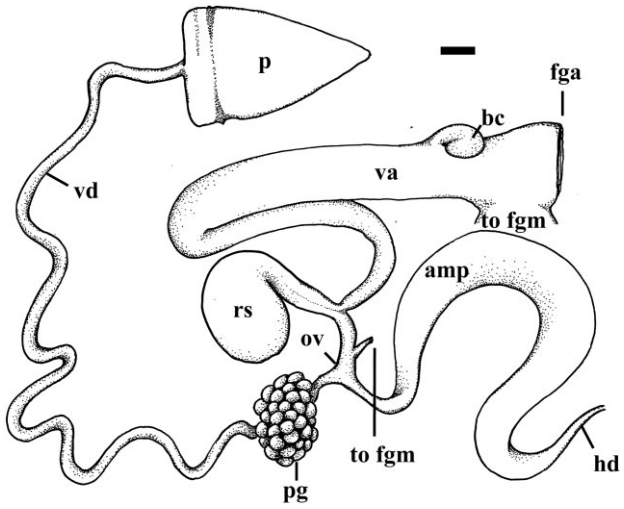

Figure 23. Reproductive system of *Dendronotus robustus* Verrill, 1870. Abbreviations: amp, ampulla; bc, bursa copulatrix; fga, female genital aperture; fgm, female gland mass; hd, hermaphroditic duct; ov, oviduct; p, penis; pg, prostate; rs, receptaculum seminis; va, vagina; vd, vas deferens. Scale bar: 1 mm.

Colour (Figs 20, 21)
Background colour red, reddish brown, or brown, sprinkled with small light-yellow or white spots. Foot white. Apices of veil papillae and dorsal appendages often with opaque white pigment. Rhinophores similar in colour to body.

Jaws (Fig. 6G)
Length of jaw approximately two times longer than width. Dorsal process length about one-third length of jaw body. Inclined posteriorly at about 15°. Masticatory process is about six times smaller than body. Masticatory border with single row of rodlets.

Radula (Fig. 22)
Radula formula: 30 × 10–11.1.10–11 (ZMMU Op-346); 25 × 7–9.1.7–9 (ZMMU Op-347); 31 × 8–10.1.8–10 (ZMMU Op-343); 28 × 7–9.1.7–9 (ZMMU Op-348). Median tooth large, triangular, with well-differentiated conical cusp (Fig. 22A, B, D, E). Bearing between ten and 18 small denticles on each side. Furrows strong. Lateral teeth triangular and elongate, with cusp lacking denticles, some teeth with two cusps (Fig. 22A, C, E, F). Outer teeth subulate and thin. Juvenile median tooth with numerous denticles, cusp reduced (Fig. 22G). Laterals elongate and slightly curved, smooth or with between four and eight denticles.

Reproductive system (Fig. 23)
Triaulic. Ovotestis large, composed from many rounded yellow lobules. Hermaphroditic duct expands into wide winding ampulla. Prostata consists of nuemrous oval alveoli, distal part of vas deferens wide and expands to stout triangular penis. Oviduct connects through insemination duct into female gland complex. Vagina long and convoluted, with small bursa copulatrix, tapers along its length, and ending in rounded seminal receptaculum. Female genital aperture opens posterior to penis on right side of body, between first and second pairs of dorsolateral processes.

Ecology
Inhabits muddy sands from upper subtidal zone down to at least 240 m in depth. Feeds on polychaetes, hydroids, and probably other bottom material that it collects from the sediment surface with wide oral veil (Roginskaya, 1990). The reproduction occurs in August–September. Egg mass is large entangled narrow cord. Veliger is planktotrophic with oval shell.

Distribution
Circumpolar Arctic species. Has also been found in the north-west Atlantic and in the northern Pacific. In Russian waters, has been found in the White Sea, the Barents Sea, the Kara Sea, and in the Bering Strait.

Remarks
Georg Sars described a new species *Dendronotus velifer* Sars, 1878 off Finmarken coast of the Barents Sea (100–200 m depth). It is still commonly considered as a junior synonym of *D. robustus* Verrill, 1870; however, the present study reveals some morphological and molecular heterogeneity of *D. robustus*. For example, in the Barents Sea *D. robustus* tends to separate into shallow water (4–10 m) and deep sea (100–200 m) populations. Shallow water specimens are brown or reddish brown, whereas most of the deep-sea specimens are red or dark pink. Radular morphology also demonstrates some minor differences concerning the variability of the rachidian tooth cusp proportions and presence of denticles on the lateral teeth. Preliminary molecular data also show some differentiation between shallow waters and deep-sea specimens. Some transitional forms at intermediate depths (50–100 m) were discovered, however. Therefore, to resolve the question of whether *D. velifer* and *D. robustus* are separate species or not, an additional morphological and molecular study is necessary. The conspecificity between west and east Atlantic *D. robustus* also needs to be confirmed.

Molecular results

Phylogenetic analysis
We acquired 220 original nucleotide sequences for 56 specimens covering seven species of the genus *Dendronotus* (Table 1). The combined data set

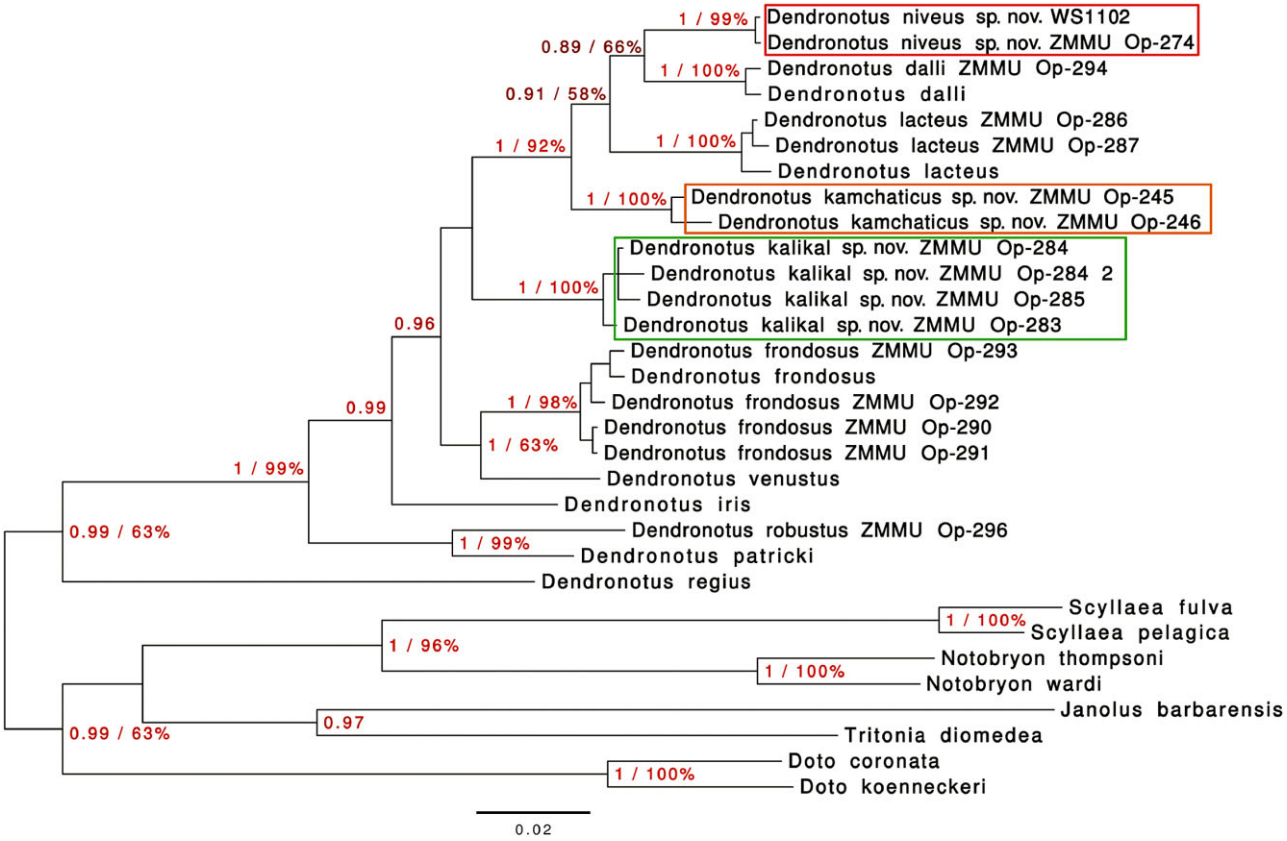

Figure 24. Phylogenetic hypothesis based on combined molecular data (*COI* + *16S* + *H3* + *28S*) represented by Bayesian inference. First numbers on branches represent posterior probabilities from Bayesian inference. Second numbers indicate bootstrap values for maximum likelihood.

including four loci was presented in a sequence alignment of 1791 codon positions. Single-gene trees based on mitochondrial DNA and combined gene trees showed rather poor support in sister-group relationships, whereas species-level clades had high support (Figs S2, S3; combined tree not shown). *H3* and *28S* trees revealed low divergence between species (as previously described, as well as among new species), which could be explained by the slow rates of gene evolution (Figs S4, S5; combined tree not shown). So these markers are more appropriate for phylogenetic analysis than for species delimitation. Nevertheless, the results of nuclear gene analyses do not refute our species hypothesis. To exclude the possibility of finding hybrids within analysed species, we studied specimens from different populations in large numbers. Moreover, preliminary data on *18S* rRNA (unpublished) confirmed the species-level clades distinguished by mitochondrial DNA analysis.

The concatenated trees of four markers analysed separately presented high support and good resolution. The topology of the tree based on Bayesian analysis was congruent with the results of the maximum-likelihood (ML) tree, so the ML tree is not shown. Our phylogenetic reconstructions confirm *Dendronotus* monophyly and consistently group it with other Dendronotida (Figs 24, S1). Node support values for both ML and Bayesian inferences were mostly high, and both had the same topology (posterior probability, PP = 1; bootstrap values, BS = 78%). Our data show that all *D. frondosus* specimens from the White and the Barents seas belong to the same species, disregarding their colour variations (PP = 1, BS = 99%). Nucleotide sequences of *COI*, *16S*, and *H3* of all these specimens match each other and sequences of samples from northern Scotland. We also confirmed *D. lacteus* findings from the Barents Sea, not previously counted among *Dendronotus* in Russian fauna. All *D. lacteus* specimens from all regions, including those with 'reddish brown with white spots', form a consistent clade (PP = 1, BS = 100%). *Dendronotus kamchaticus* sp. nov. and *D. kalikal* sp. nov. from north-west Pacific waters are clearly separated in all our reconstructions. On a larger scale, *D. kalikal* sp. nov. is separated from a clade formed by *D. kamchaticus* sp. nov., *D. lacteus*, *D. niveus* sp. nov., and *D. dalli* (PP = 1, BS = 100; PP = 1, BS = 94,

respectively), despite being morphologically similar to *D. kamchaticus* sp. nov. *Dendronotus frondosus* and *D. venustus* are genetically highly divergent from *D. kamchaticus* sp. nov. and *D. kalikal* sp. nov., but are seemingly close morphologically. *Dendronotus dalli* and *D. niveus* sp. nov. are consistently separate on all of our trees, and therefore molecular data confirm *D. niveus* sp. nov. from the White and the Barents seas, formerly considered to be *D. dalli*, as a new species (PP = 1, BS = 100%). *Dendronotus dalli* from the north-east Pacific is very close to the *D. dalli* sample from GenBank (PP = 1, BS = 100%); however, the origin of latter sample (east Atlantic) is inconsistent with the known habitat of this species. *Dendronotus robustus*, inhabiting depths of up to 240 m, turned out to be a sibling species of deep-water *D. patricki* from the Pacific Ocean (PP = 1, BS = 99%). Both tropical species *D. regius* and *D. orientalis* (only *16S* and *H3* data sets) are in the stem of the genus. This may indicate a single event in the formation of boreal species from one ancestor, but to confirm this more data from tropical species must be included in the analysis.

Species delimitation

The ABGD analysis of the *COI* data set run with two different models revealed 12 clades each: one for *D. robustus*, one for *D. frondosus*, one for *D. lacteus*, one for *D. kalikal* sp. nov., one for *D. kamchaticus* sp. nov., one for *D. niveus* sp. nov., one for *D. dalli*, one for *D. venustus*, one for *D. iris*, one for *D. albopunctatus*, one for *D. patricki*, and one for *D. regius*. The ABGD analysis of the *16S* data set revealed 16 clades each: one for *D. robustus*, one for *D. frondosus*, one for *D. lacteus*, one for *D. kalikal* sp. nov., one for *D. kamchaticus* sp. nov., one for *D. niveus* sp. nov., one for *D. dalli*, one for *D. venustus*, one for *D. iris*, one for *D. albus*, one for *D. orientalis*, one for *D. patricki*, one for *D. subramosus*, one for *D. rufus*, and one for *D. regius*. The prior maximum distance ranged between 0.001 and 0.0123 for *COI*. In the case of *16S* the prior maximum distance ranged between 0.0025 and 0.0067. Therefore, the results of the ABGD analysis confirmed the species hypothesis of both molecular phylogenetic analysis (i.e. concatenated and single gene trees) and morphological data.

DISCUSSION

The present morphological analysis reveals seven species of the genus *Dendronotus* inhabiting the cold waters of Eurasia. A molecular phylogenetics hypothesis (Fig. 24) based on the four genes (*COI*, *16S* rRNA, *H3*, and *28S* rRNA) confirms the morphological data. The ABGD analysis of two loci (*COI* and *16S*) and single gene-tree analyses of three loci (*COI*, *16S*, and *18S*) are congruent with morphological data and the concatenated phylogenetic tree. Two loci of nuclear genes *H3* and *28S* rRNA showed low divergence, so they are not appropriate for molecular species delimitation, at least within *Dendronotus*, but can be used for phylogenetic reconstructions within genera or even within Dendronotina.

One of the most common species *D. frondosus* was previously considered (Odhner, 1936; Robilliard, 1970; Thompson & Brown, 1984; Roginskaya, 1987; Baba, 1993) to have a very broad geographical range, encompassing almost all of the Northern and Arctic seas; however, according to the present study *D. frondosus* is restricted only to the North Atlantic boreal and subarctic waters. This result thus corroborates recent analysis (Stout *et al*., 2010) that revealed the separate species status of the *D. venustus* MacFarland, 1966 in the Easteren Pacific. The latter species was also, for a long time, considered as a synonym of *D. frondosus*. This highly variable species commonly inhabits the coastal shallow waters of the subarctic Barents and White seas (Figs 1–4); however, both radular morphology and molecular analysis consistently reveal all variously coloured specimens as a single species (Figs 24, S1). In the north-west Pacific we found the opposite situation. The present study uncovers the presence in this region of two new species externally similar to the North Atlantic *D. frondosus*, but significantly differing according to the four-gene analysis and radular morphology.

Dendronotus dalli was previously considered as an amphiboreal and even circumpolar species (e.g. Roginskaya, 1987). The present study, for the first time, clearly shows that all records of *D. dalli* from the North Atlantic belong to a new species: *D. niveus* sp. nov. The latter differs from *D. dalli* according to the molecular data, morphology of the dorsal appendages, and body coloration. Thus, this study does not confirm the amphiboreal status of the two common species *D. frondosus* and *D. dalli*. These two species are restricted to the North Atlantic and the North Pacific, respectively. The discovery of two sympatric species, *D. kamchaticus* sp. nov. and *D. kalikal* sp. nov., in the north-west Pacific is important for taxonomic and biogeographic studies because it raises a question about the validity of many amphiboreal species.

Previously, in the North Atlantic almost all variously coloured specimens have been considered within the single species *D. frondosus*. Only relatively recently an analysis based on protein electrophoresis data confirmed the separate status of a neglected species *D. lacteus* from western Sweden (Thollesson, 1998). This decision was further confirmed by *16S* gene data from specimens collected close to the type locality in the Irish Sea (Stout *et al*., 2010); however, until recently the geographical range of this species remained unclear. In European waters *D. lacteus* is commonly still

KEY TO NORTHERN AND ARCTIC SPECIES OF THE GENUS *DENDRONOTUS*

1. Body narrow, high, laterally compressed. Oral veil moderate in size. Rhinophoral sheaths bear lateral papilla.... 2
– Body broad, low, dorsoventrally compressed. Oral veil large. Rhinophoral sheath without lateral papilla..... ....*Dendronotus robustus*, circumpolar species
2. Primary branches of dorsal processes short, bulbous. Tertiary branches of dorsal papillae absent or strongly reduced. Colour variegated....***Dendronotus kamchaticus* sp. nov.**, north-west Pacific
– Primary branches of dorsal processes elongated, pointed. Tertiary branches of dorsal papillae well defined. Body colour uniform or variegated....3
3. Apical parts of primary branches of dorsal processes almost smooth, without secondary and tertiary branches. White opaque pigment covers surface of the apical parts of primary branches. Body colour always uniform, light, without spots or stripes. Central teeth of the adult specimens completely smooth..... ....*Dendronotus dalli*, north-west and north-east Pacific
– Apical parts of primary branches of dorsal processes with well-defined secondary and tertiary branches. White opaque pigment, if present, on inside dorsal processes....4
4. Secondary and tertiary branches of dorsal processes rounded. Colour variegated or uniform. Rachidian teeth of adult specimens strongly denticulated. Lateral teeth bear large comb-shaped denticles..... ....*Dendronotus frondosus*, North Atlantic
– Secondary and tertiary branches of dorsal processes pointed....5
5. Apical parts of primary branches of dorsal processes distinct, with short spiniform papillae. Secondary branches absent or reduced. White opaque pigment placed inside of dorsal processes. Body colour uniform, semitransparent. Rachidian teeth of the adult specimens completely smooth..... ....***Dendronotus niveus* sp. nov.**, North Atlantic
– Apical parts of primary branches of dorsal processes indistinct, with long secondary branches. Body colour uniform or variegated, opaque. Rachidian teeth of adult specimens denticulated....6
6. Secondary branches of dorsal processes reach half of the length of primary branches. Tertiary branches and short spiniform papillae few in number. Body colour with distinct dorsal bands. Lateral teeth bear large comb-shaped denticles....***Dendronotus kalikal* sp. nov.**, north-west Pacific
– Secondary branches of dorsal processes considerably shorter than primary branches. Tertiary branches and short spiniform papillae numerous. Body colour variable but digestive gland not visible, even in uniformly coloured specimens. Lateral teeth bearing two or three small denticles, commonly completely smooth..... ....*Dendronotus lacteus*, North Atlantic and Arctic

misidentified with *D. frondosus*. This study for the first time confirms both the morphological and the molecular identity of *D. lacteus* from boreal European waters, and from the Arctic Spitsbergen and east Barents Sea.

This study reveals the essential similarity of the shape of radular teeth in early juvenile specimens of different species of the genus *Dendronotus* (Fig. 25). Potentially, this underestimated ontogenetic data may considerably affect the current systematics of the genus *Dendronotus* because radular patterns are important taxonomic characters. For instance, Robilliard (1970) and Roginskaya (1987) have reported the denticulated, *D. frondosus*-like central teeth of the radula in the species *D. dalli* and *D. niveus* sp. nov., which possess completely smooth adult central teeth (Fig. 19). Such data obviously challenge the importance of radular morphology for taxonomy. The present study uncovers the source of such variability: the anterior, oldest radular rows may retain the ontogenetically earliest teeth (Fig. 25A, D, G), which are always denticulated. In a similar way, the "genus" *Campaspe* was based (Bergh, 1863) on juvenile features (sligthly branched dorsal appendages and few rows of the lateral teeth of radula) of species of the genus *Dendronotus*. Thus the underestimation of the developmental data may mislead the taxonomy and phylogenetics of a group (Martynov & Schrödl, 2011).

The present study thus suggests an integrative framework (including morphological, ontogenetic, and molecular data) for taxonomic and phylogenetic studies of the common northern nudibranch of the genus *Dendronotus* and other opisthobranch molluscs.

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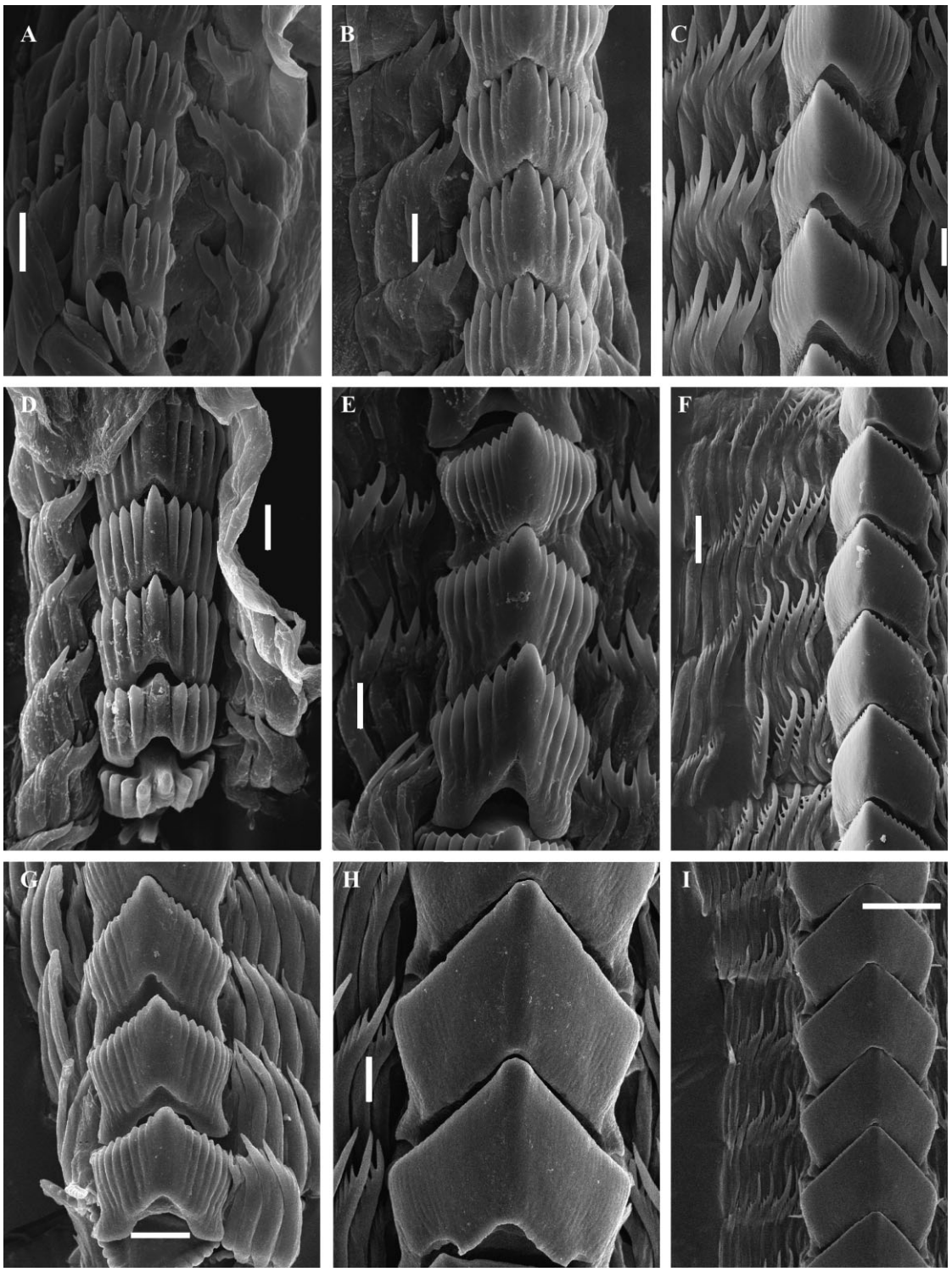

Figure 25. Common early stages of radula development and divergence of the adult radular morphology in different species of the genus *Dendronotus*. Scanning electron micrographs: A, D, early postlarval stages of the radula development (body length = 2–3 mm); B, E, G, juvenile radula (body length = 5 mm); H, subadult radula (body length = 20 mm); C, F, I, adult radula (body length = 12 mm, 10 mm and 60 mm respectively). A–C, ontogenetic series of radula development in *Dendronotus frondosus* Ascanius, 1774; D–F, ontogenetic series of radula development in ***Dendronotus kalikal* sp. nov.**; G–I, ontogenetic series of radula development in ***Dendronotus niveus* sp. nov.** Scale bars: A–E = 10 μm; F = 30 μm; G, H = 20 μm; I = 50 μm.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Figure S1. Phylogenetic hypothesis based on combined molecular data (*COI* + *16S* + *H3* + *28S*), represented by Bayesian inference, and including all specimens.
Figure S2. Phylogenetic tree based on *COI* alignment, represented by Bayesian inference.
Figure S3. Phylogenetic tree based on *16S* alignment, represented by Bayesian inference.
Figure S4. Phylogenetic tree based on *H3* alignment, represented by Bayesian inference.
Figure S5. Phylogenetic tree based on *28S* alignment, represented by Bayesian inference.
Table S1. Available sequences of *Dendronotus* and out-groups retrieved from GenBank.